Downloaded from orbit.dtu.dk on: May 06, 2023

DTU Library

A taxonomic and phylogenetic revision of Penicillium section Aspergilloides

Houbraken, J.; Visagie, C.M.; Meijer, M.; Frisvad, Jens Christian; Busby, P.E.; Pitt, J.I.; Seifert, K.A.; Louis-Seize, G.; Demirel, R.; Yilmaz, N.

Total number of authors:
13

Published in:
Studies in Mycology

Link to article, DOI:
10.1016/j.simyco.2014.09.002

Publication date:
2014

Document Version
Publisher's PDF, also known as Version of record

Link back to DTU Orbit

Citation (APA):
Houbraken, J., Visagie, C. M., Meijer, M., Frisvad, J. C., Busby, P. E., Pitt, J. I., Seifert, K. A., Louis-Seize, G., Demirel, R., Yilmaz, N., Jacobs, K., Christensen, M., & Samson, R. A. (2014). A taxonomic and phylogenetic revision of Penicillium section Aspergilloides. *Studies in Mycology*, *78*, 373-451. https://doi.org/10.1016/j.simyco.2014.09.002

General rights
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

available online at www.studiesinmycology.org

STUDIES IN MYCOLOGY 78: 373–451.

A taxonomic and phylogenetic revision of *Penicillium* section *Aspergilloides*

J. Houbraken[1*], C.M. Visagie[1], M. Meijer[1], J.C. Frisvad[2], P.E. Busby[3], J.I. Pitt[4], K.A. Seifert[5], G. Louis-Seize[5], R. Demirel[6], N. Yilmaz[1], K. Jacobs[7*], M. Christensen[8], and R.A. Samson[1]

[1]*CBS-KNAW Fungal Biodiversity Centre, Uppsalalaan 8, NL-3584 CT Utrecht, The Netherlands;* [2]*Department of Systems Biology, Building 221, Technical University of Denmark, DK-2800 Kgs. Lyngby, Denmark;* [3]*Department of Biology, Stanford University, 371 Serra Mall, Stanford, CA 94305, USA;* [4]*CSIRO Animal, Food and Health Sciences, North Ryde, NSW 2113, Australia;* [5]*Biodiversity (Mycology), Agriculture & Agri-Food Canada, Ottawa, ON K1A 0C6, Canada;* [6]*Department of Biology, Faculty of Science, Anadolu University, Turkey;* [7]*Department of Microbiology, University of Stellenbosch, Private Bag X1, Stellenbosch 7600, South Africa;* [8]*Botany Department, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA*

**Correspondence*: J. Houbraken, j.houbraken@cbs.knaw.nl; K. Jacobs, kj@sun.ac.za

Abstract: Species belonging to *Penicillium* section *Aspergilloides* have a world-wide distribution with *P. glabrum*, *P. spinulosum* and *P. thomii* the most well-known species of this section. These species occur commonly and can be isolated from many substrates including soil, food, bark and indoor environments. The taxonomy of these species has been investigated several times using various techniques, but species delimitation remains difficult. In the present study, 349 strains belonging to section *Aspergilloides* were subjected to multilocus molecular phylogenetic analyses using partial β-tubulin (*BenA*), calmodulin (*CaM*) and RNA polymerase II second largest subunit (*RPB2*) sequences. Section *Aspergilloides* is subdivided into 12 clades and 51 species. Twenty-five species are described here as new and *P. yezoense*, a species originally described without a Latin diagnosis, is validated. Species belonging to section *Aspergilloides* are phenotypically similar and most have monoverticillate conidiophores and grow moderately or quickly on agar media. The most important characters to distinguish these species were colony sizes on agar media, growth at 30 °C, ornamentation and shape of conidia, sclerotium production and stipe roughness.

Key words: *Eurotiales*, Soil fungi, Multigene phylogeny, ITS barcoding.
Taxonomic novelties: *Penicillium armarii* Houbraken, Visagie, Samson & Seifert, *P. athertonense* Houbraken, *P. austroafricanum* Houbraken & Visagie, *P. brunneoconidiatum* Visagie, Houbraken & K. Jacobs, *P. bussumense* Houbraken, *P. cartierense* Houbraken, *P. clavistipitatum* Visagie, Houbraken & K. Jacobs, *P. contaminatum* Houbraken, *P. flavisclerotiatum* Visagie, Houbraken & K. Jacobs, *P. grevilleicola* Houbraken & Quaedvlieg, *P. hoeksii* Houbraken, *P. infraaurantiacum* Visagie, Houbraken & K. Jacobs, *P. kiamaense* Houbraken & Pitt, *P. longicatenatum* Visagie, Busby, Houbraken & K. Jacobs, *P. malmesburiense* Visagie, Houbraken & K. Jacobs, *P. pulvis* Houbraken, Visagie, Samson & Seifert, *P. ranomafanaense* Houbraken & Hagen, *P. rudallense* Houbraken, Visagie & Pitt, *P. sterculiniicola* Houbraken, *P. sublectaticum* Houbraken, Frisvad, Samson & Seifert, *P. subspinulosum* Houbraken, *P. tsitsikammaense* Houbraken, *P. turcosoconidiatum* Visagie, Houbraken & K. Jacobs, *P. vagum* Houbraken, Pitt, Visagie & K. Jacobs, *P. verhagenii* Houbraken, *P. yezoense* Hanzawa ex Houbraken.

Published online 22 September 2014; http://dx.doi.org/10.1016/j.simyco.2014.09.002. Hard copy: June 2014.

INTRODUCTION

In the classification of Raper & Thom (1949), Penicillia that produce monoverticillate conidiophores were placed in the *Monoverticillata* group. They divided this group into nine series based on colony texture, production of sclerotia and/or cleistothecia and length of conidiophores. A series of species with irregularly branched conidiophores was also included in this classification, namely series *Ramigena fide* Raper & Thom. Pitt (1980) later excluded this series from his circumscription of subgenus *Aspergilloides*. In Pitt's classification, subgenus *Aspergilloides* only included species in which the majority of conidiophore stipes are well defined and terminate in monoverticillate penicilli (Pitt 1980). Additionally, he introduced sections *Aspergilloides* and *Exilicaulis* in subgenus *Aspergilloides* based on the presence or absence of a swelling at the stipe apex. Peterson (2000) was among the first to study the infrageneric relations in *Penicillium* using DNA sequence data. Based on a phylogeny of nrDNA sequences, the genus was divided into six groups with group 2 containing species mainly belonging to Pitt's section *Aspergilloides* (*P. glabrum*, *P. purpurescens*, *P. spinulosum*, *P. fuscum* (syn. *E. pinetorum*), *P. thomii*, *P. lividum*, *P. lapidosum* (syn. *E. lapidosum*) and *P. asperosporum*). Houbraken & Samson (2011) studied the phylogeny of *Penicillium* in more detail using a combined data set of four genes. Based on the inferred phylogenetic relationships among the Penicillia, they proposed a sectional classification and subdivided *Penicillium* into two subgenera and 25 sections, with section *Aspergilloides* being one of them. With exception of *P. lapidosum*, all species assigned to Peterson's group 2 were included in the re-circumscribed section *Aspergilloides* and an additional twelve species were included. The majority of species belonging to section *Aspergilloides* are predominantly monoverticillate and most grow quickly on agar media (Pitt 1980, Houbraken & Samson 2011).

The most well-known species in section *Aspergilloides* are *P. glabrum* and *P. spinulosum*. Phenotype-based identification of these species is problematic and the taxonomy has been studied several times. Raper & Thom (1949) distinguished *P. spinulosum* from *P. glabrum* based on colony texture: the colony surface of *P. spinulosum* was stated to be "loose textured" while *P. glabrum* was "strictly velvety". This distinction was also adopted by Ramírez (1982). Pitt (1980) primarily separated *P. glabrum* from *P. spinulosum* by conidial wall texture, which was stated to be "smooth or at most finely roughened" for *P. glabrum* and "rugose or spinose" for *P. spinulosum*. However, *P. spinulosum* isolates

Peer review under responsibility of CBS-KNAW Fungal Biodiversity Centre.
Copyright © 2014, CBS-KNAW Fungal Biodiversity Centre. Production and hosting by ELSEVIER B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/3.0/).

with smooth to finely roughened conidia were also accepted in his definition of the species, and then the floccose texture of the colony was the key character to separate *P. spinulosum* from *P. glabrum*. In 1990, the Subcommission on *Penicillium* and *Aspergillus* Systematics (SPAS, currently known as the International Commission on *Penicillium* and *Aspergillus*, ICPA) investigated the taxonomy of *P. glabrum*, *P. spinulosum* and the related species *P. purpurescens* and *P. montanense* (Pitt *et al.* 1990). Colony diameters on Czapek yeast extract agar (CYA) and 25 % glycerol nitrate agar (G25N), conidial wall texture and width of the phialides proved to be valuable characters for the identification of these species. However, four of the 15 strains could not be identified, indicating the difficulty of a phenotype-based identification of these species and/or the presence of cryptic species. Although *P. spinulosum*, *P. glabrum*, *P. purpurescens* and *P. montanense* are difficult to distinguish phenotypically, Peterson (2000) could identify them based on nrDNA sequences. These species were closely related in their nrDNA (ITS barcode, including partial LSU) sequences, but displayed 4–8 nucleotide substitutions between each of the pairings. The taxonomy of the "*Penicillium glabrum* complex" was also studied using partial β-tubulin and calmodulin sequences (Barreto *et al.* 2011). Based on this data, *P. glabrum* and *P. spinulosum* could be clearly distinguished.

In this study, we delimitate *Penicillium* section *Aspergilloides* using a phylogenetic analysis of a combined data set of partial β-tubulin (*BenA*), calmodulin (*CaM*) and RNA polymerase II second largest subunit (*RPB2*) gene sequences. Subsequently, the phylogenetic relationships among species of section *Aspergilloides* were investigated and species limits were proposed based on the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) concept (Taylor *et al.* 2000), supplemented with physiological and macro- and microscopic characters. We included 349 strains assigned to section *Aspergilloides* in our analyses, including type and freshly isolated strains. ITS barcodes were generated and investigated for their suitability for species identification.

MATERIAL AND METHODS

Fungal strains

Isolates were obtained from different culture collections (CBS, CBS-KNAW Fungal Biodiversity Centre, Utrecht, the Netherlands; IBT, culture collection of the DTU Systems Biology, Lyngby, Denmark; and FRR, culture collection of CSIRO Animal, Food and Health Sciences, North Ryde, Australia). Fresh isolates deposited in the working collection of the Department of Applied and Industrial Mycology (DTO), housed at CBS, were also included in this study and a selection of those strains were accessioned to the CBS culture collection. An overview of strains is listed in Table 1.

DNA extraction, PCR and sequencing

Strains were grown for 3–14 d on MEA prior to DNA extraction. DNA was extracted using the Ultraclean™ Microbial DNA isolation Kit (MoBio, Solana Beach, U.S.A.) and the extracted DNA was stored at −20 °C. The nuclear ribosomal internal transcribed spacer regions (ITS1-5.8S-ITS2) and parts of the *BenA*, *CaM* and *RPB2* genes were amplified and sequenced using methods previously described (Houbraken & Samson 2011, Houbraken *et al.* 2012a, b, Frisvad *et al.* 2013).

Phylogenetic analysis

Section *Aspergilloides* was delimitated using a data set combining *BenA*, *CaM* and *RPB2*. The ITS sequences had a low phylogenetic signal and this data was only examined for its applicability in species recognition in the context of DNA barcoding. The phylogeny of individual clades within section *Aspergilloides* was studied both by comparing single gene phylogenies, to determine whether groups of strains could be recognised as independent evolutionary lineages, and by concatenated analyses of the three genes to resolve relationships among the species. Maximum likelihood (ML) and Maximum Parsimony (MP) analyses were performed using MEGA5 and were applied to most individual *BenA*, *CaM* and *RPB2* data sets. Exceptions were the *P. spinulosum*- and *P. glabrum*-clade data sets, where ML and Bayesian analysis was applied. The robustness of tree topology for each analysis was evaluated by 1 000 bootstrap replicates. All combined data sets were analysed using the RAxML (randomised accelerated maximum likelihood) (Stamatakis *et al.* 2008) and Bayesian tree inference (BI) analyses using MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003). Prior to analyses, the most suitable substitution model was determined using MrModeltest v. 3.1.2 (Nylander 2004), utilising the Akaike information criterion (AIC). Bayesian analyses were performed with two sets of four chains (one cold and three heated) and the STOPRULE option, stopping analyses at an average standard deviation of split frequencies of 0.01. The sample frequency was set to 100 and the first 25 % of trees were removed as burn-in. The different loci within the combined data sets were analysed as separate partitions. *Penicillium expansum* ATCC 24692, a member of subgenus *Penicillium* section *Penicillium*, was used as outgroup for all analyses. The phylograms were redrawn and annotated using Adobe Illustrator CS5. BI posterior probabilities (pp) values and bootstrap (bs) percentages of the maximum likelihood (ML) analysis are presented at the nodes. Values less than 0.95 pp and less than 70 % bs are not shown. Branches with more than 95 % bs and 1.00 pp are thickened. Newly obtained sequences were deposited in GenBank under accession numbers KM088669–KM089827.

ITS barcoding

The ITS sequence diversity of strains belonging to section *Aspergilloides* was assessed by determining the number of haplotypes among the ITS sequences. The software programme DnaSP v. 5.10 (Librado & Rozas 2009) was used to find the different haplotypes in the alignment. Gaps and missing data were included in this calculation. ITS sequences were deposited in GenBank under accession numbers KM189445–KM189803.

Phenotypic examination

Macroscopic characters were studied on the agar media Czapek yeast extract agar (CYA), malt extract agar (MEA; Oxoid), creatine sucrose agar (CREA), dichloran 18 % glycerol agar (DG18), yeast extract sucrose agar (YES), oatmeal agar (OA)

Table 1. Strains used in this study.

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. ardesiacum	DTO 093-C1 = CBS 497.73 = ATCC 24719 = FRR 1479 = IFO 30540 = IMI 174719 = VKM F-1749	Stems of *Vitis vinifera* during drying; Alma-Ata Region, Kazachstan; ex-neotype of *P. ardesiacum*	KM189565	KM088805	KM089577	KM089190
P. armarii	DTO 235-F1 = CBS 138171	House Dust; Hobart, Australia; ex-type of *P. armarii*	KM189758	KM089007	KM089781	KM089394
	DTO 235-F3	House Dust; Hobart, Australia	KM189759	KM089008	KM089782	KM089395
	DTO 236-D3	House Dust; Hobart, Australia	KM189760	KM089009	KM089783	KM089396
P. athertonense	DTO 030-C2 = CBS 138161	Forest soil (wet); Atherton Tableland, Queensland, Australia	KM189462	KM088690	KM089462	KM089075
P. aurantioviolaceum	DTO 225-E4 = CBS 137777 = NRRL 762	Unrecorded source; Puerto Rico; ex-neotype of *P. aurantioviolaceum*	KM189756	KM089005	KM089779	KM089392
	DTO 091-A1 = CBS 347.59 = FAT 340 = IFO 6031 = IMI 068221	Soil; Japan; ex-type of *P. thomii* var. *flavescens* nom. inval.	KM189552	KM088791	KM089563	KM089176
	DTO 085-A7	Soil, 2 mtr. from road; Ranoma fana, Madagascar	KM189542	KM088780	KM089552	KM089165
	DTO 253-H3 = CBS 137779	Leaves; Zambia	KM189763	KM089012	KM089786	KM089399
P. austroafricanum	DTO 133-G5 = CBS 137773	Leaf of *Phaenocoma prolifera*; Harold Porter Botanical Garden Western Cape, South Africa; ex-type of *P. austroafricanum*	KM189610	KM088854	KM089628	KM089241
	DTO 132-D6	Leaf of *Phaenocoma prolifera*; Harold Porter Botanical Garden Western Cape, South Africa	KM189609	KM088853	KM089627	KM089240
	DTO 180-E3 = CV 2851 = KAS 3946	Fynbos soil; Riverlands, South Africa	KM189637	KM088881	KM089655	KM089268
	DTO 182-B3 = CBS 137756 = CV 851 = KAS 4183 = DAOM 241138	Air sample from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189656	KM088900	KM089674	KM089287
	DTO 182-C7 = CBS 137757 = CV 905 = KAS 4197 = DAOM 241141	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189660	KM088904	KM089678	KM089291
	DTO 182-H2 = CBS 137758 = CV 1145 = KAS 3974 = DAOM 241140	Mite inside *Protea repens* infructescens; Riverlands, Malmesbury, Western Cape, South Africa	KM189674	KM088919	KM089693	KM089306
	DTO 182-H3 = CBS 137759 = CV 1148 = KAS 3975 = DAOM 241139	Mite inside *Protea repens* infructescens; Riverlands, Malmesbury, Western Cape, South Africa	KM189675	KM088920	KM089694	KM089307
P. brunneoconidiatum	DTO 182-E4 = CBS 137732 = CV 949 = KAS 4214 = DAOM 241359	Soil; Fynbos, Riverlands, Malmesbury, Western Cape, South Africa; ex-type of *P. brunneoconidiatum*	KM189666	KM088911	KM089685	KM089298
	DTO 182-B7 = CV 875 = KAS 4187	Fynbos soil; Riverlands, South Africa	KM189657	KM088901	KM089675	KM089288
	DTO 182-C6 = CV 901 = KAS 4196	Fynbos soil; Riverlands, South Africa	KM189659	KM088903	KM089677	KM089290
	DTO 182-D8 = CV 935 = KAS 4209	Fynbos soil; Riverlands, South Africa	KM189663	KM088908	KM089682	KM089295
	DTO 182-E2 = CV 946 = KAS 4212	Fynbos soil; Riverlands, South Africa	KM189665	KM088910	KM089684	KM089297
	DTO 182-F2 = CV 970 = KAS 4222	Fynbos soil; Riverlands, South Africa	KM189670	KM088915	KM089689	KM089302
	DTO 185-F4 = CV 915	Fynbos soil; Riverlands, South Africa	KM189691	KM088937	KM089711	KM089324
	DTO 185-F6 = CV 921	Fynbos soil; Riverlands, South Africa	KM189692	KM088938	KM089712	KM089325
P. bussumense	DTO 018-B2 = CBS 138160	Soil; Spanderswoud, Bussum, the Netherlands; ex-type of *P. bussumense*	KM189458	KM088685	KM089457	KM089070
P. cartierense	DTO 092-H9 = CBS 137956	Heathland soil; Cartier Heide, Eersel, the Netherlands; ex-type of *P. cartierense*	KM189564	KM088804	KM089576	KM089189
	DTO 091-A6 = CBS 863.71	Agricultural soil; Wageningen, the Netherlands	KM189557	KM088796	KM089568	KM089181
P. clavistipitatum	DTO 182-E5 = CBS 138650 = CV 951 = KAS 4216 = DAOM 241125	Soil; Fynbos, Riverlands, South Africa; ex-type of *P. clavistipitatum*	KM189667	KM088912	KM089686	KM089299
	DTO 182-E8 = CV 960 = KAS 4219 = DAOM 241128	Fynbos soil; Riverlands, South Africa	KM189668	KM088913	KM089687	KM089300
	DTO 182-E9 = CV 962 = KAS 4220 = DAOM 241126	Fynbos soil; Riverlands, South Africa	KM189669	KM088914	KM089688	KM089301
P. contaminatum	DTO 091-A3 = CBS 345.52 = IMI 049057	Contaminant; Surrey, Kew, UK; ex-type of *P. contaminatum*	KM189554	KM088793	KM089565	KM089178
	DTO 296-G9 = CBS 346.59	Acidic soil; Unknown location	KM189782	KM089032	KM089806	KM089419

(*continued on next page*)

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. crocicola	DTO 104-E2 = CBS 745.70 = ATCC 18313 = QM 7778	Corm of *Crocus sativus*; Japan; ex-isotype of *P. crocicola*	KM189581	KM088824	KM089597	KM089210
	DTO 082-A9 = CBS 137772	Archive; Den Bosch, the Netherlands	KM189532	KM088770	KM089542	KM089155
	DTO 086-C2	Swab sample taken in archive; Den Bosch, the Netherlands	KM189545	KM088783	KM089555	KM089168
	DTO 090-F5	Swab sample in archive; Asperen, the Netherlands	KM189548	KM088786	KM089558	KM089171
	DTO 181-G2 = CBS 137754 = CV 461 = KAS 4133 = DAOM 241137	*Protea repens* infructescens; Stellenbosch mountain, Western Cape, South Africa	KM189651	KM088895	KM089669	KM089282
	DTO 210-F5 = CBS 132168 = WSF 2215	Soil; A1 horizon Soil; S. Wisconsin maple-elm-ash forests, deciduous forest; Wisconsin; USA	KM189750	KM088999	KM089773	KM089386
	DTO 265-H7	Grapevine; Ajabshir, Iran	KM189768	KM089018	KM089792	KM089405
	DTO 266-A4 = CBS 137780	Grapevine; Malekan, Iran	KM189769	KM089019	KM089793	KM089406
P. flavisclerotiatum	DTO 180-I1 = CBS 137749 = CV 77 = KAS 4173 = DAOM 241158	Soil from Fynbos; Stellenbosch mountain, Western Cape, South Africa; ex-type of *P. flavisclerotiatum*	KM189643	KM088887	KM089661	KM089274
	DTO 180-I8 = CBS 137750 = CV 100 = KAS 3958 = DAOM 241157	Soil from Fynbos; Stellenbosch mountain, Western Cape, South Africa	KM189644	KM088888	KM089662	KM089275
	DTO 181-H7 = CBS 137748 = CV 537 = KAS 4149 = DAOM 241156	Soil from Fynbos; Stellenbosch mountain, Western Cape, South Africa	KM189653	KM088897	KM089671	KM089284
	DTO 182-B2 = CV 839 = KAS 4181 = DAOM 241155	Air sample; Riverlands, South Africa	KM189655	KM088899	KM089673	KM089286
	DTO 182-D3 = CV 924 = KAS 4203 = DAOM 241154	Fynbos soil; Riverlands, South Africa	KM189661	KM088906	KM089680	KM089293
	DTO 182-D4 = CBS 137751 = CV 925 = KAS 4204 = DAOM 241153	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189662	KM088907	KM089681	KM089294
	DTO 182-D9 = CBS 137752 = CV 938 = KAS 4210 = DAOM 241152	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189664	KM088909	KM089683	KM089296
	DTO 182-F3 = CBS 137753 = CV 971 = KAS 4223 = DAOM 241151	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189671	KM088916	KM089690	KM089303
	DTO 184-D8 = CV 65	Fynbos soil; Stellenbosch, South Africa	KM189686	KM088932	KM089706	KM089319
	DTO 184-D9 = CV 76	Fynbos soil; Stellenbosch, South Africa	KM189687	KM088933	KM089707	KM089320
	DTO 184-E1 = CV 80	Fynbos soil; Stellenbosch, South Africa	KM189688	KM088934	KM089708	KM089321
	DTO 185-A5 = CV 545	Fynbos soil; Stellenbosch, South Africa	KM189689	KM088935	KM089709	KM089322
	DTO 185-B1 = CV 553	Fynbos soil; Stellenbosch, South Africa	KM189690	KM088936	KM089710	KM089323
P. frequentans	DTO 070-E4 = CBS 105.11	Unrecorded source; ex-type of *P. frequentans*	KM189525	KM088762	KM089534	KM089147
	DTO 070-E2 = CBS 229.28 = FRR 751 = IMI 092231 = MUCL 29111 = NRRL 751	Soil under conifer; Poland; ex-type of *P. paczowskii*	KM189524	KM088761	KM089533	KM089146
	DTO 053-F2 = IBT 5635	Citrus extract; Denmark	KM189485	KM088722	KM089494	KM089107
	DTO 053-F3 = IBT 6178	Unknown source; Denmark	KM189486	KM088723	KM089495	KM089108
	DTO 053-F4 = IBT 6422	Indoor air; Denmark	KM189487	KM088724	KM089496	KM089109
	DTO 053-F5 = IBT 6552 = NRRLA-23305	Barley; Denmark	KM189488	KM088725	KM089497	KM089110
	DTO 053-F6 = IBT 18381 = CCRC 32565	Melon seed; Hsinchu City, Taiwan	KM189489	KM088726	KM089498	KM089111
	DTO 053-F8 = IBT 23011	Air of margarin factory; Vejle, Denmark	KM189491	KM088728	KM089500	KM089113
	DTO 053-G1 = IBT 23188	Saltern; Secovlje salt pans, Slovenia	KM189492	KM088729	KM089501	KM089114
	DTO 053-G2 = IBT 23304	Artic soil; Svalbard, Norway	KM189493	KM088730	KM089502	KM089115
	DTO 053-G3 = IBT 24700	Air of factory; Sweden	KM189494	KM088731	KM089503	KM089116
	DTO 053-G4 = IBT 24773	Saltern; Secovlje salt pans, Slovenia	KM189495	KM088732	KM089504	KM089117
	DTO 053-G5 = IBT 24777	Saltern; Secovlje salt pans, Slovenia	KM189496	KM088733	KM089505	KM089118
	DTO 053-G6 = IBT 26406	Ice; Pakitsoq, Greenland	KM189497	KM088734	KM089506	KM089119
	DTO 053-G7 = IBT 26412	Ice; Pakitsoq, Greenland	KM189498	KM088735	KM089507	KM089120
	DTO 055-B9	Indoor enviroment; Munchen, Germany	KM189499	KM088736	KM089508	KM089121

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. frequentans	DTO 174-A2 = CBS 138169	Leaf of *Eucalyptus* species; Lavers hill, Tasmania, Australia	KM189620	KM088864	KM089638	KM089251
	DTO 249-D1	Artichoke; Finland	KM189762	KM089011	KM089785	KM089398
P. fuscum	DTO 111-B7 = CBS 127833 = HDAUPII-06-9026	Soil; Sichuan Prov., Kangding County; ex-type of *Eladia inflata*	KM189586	KM088830	KM089603	KM089216
	DTO 078-F6 = CBS 203.87 = IBT 16267	Sandy soil collected on the shore of the Beagle Channel; National Park of 'Lapataya' (Tierra del Fuego), Argentina; ex-type of *P. lapatayae*	KM189531	KM088768	KM089540	KM089153
	DTO 094-D7 = CBS 309.63 = ATCC 18322	Forest soil; Macedonia; ex-type of *P. macedonense*	KM189566	KM088806	KM089578	KM089191
	DTO 088-I6 = CBS 295.62 = ATCC 14770 = CCRC 31517 = DSM 2438 = IFO 7743 = IMI 094209 = MUCL 31196 = NRRL 3008 = WSF 15c	Pine-birch forest soil; Vilas County, Wisconsin, USA; ex-type of *P. pinetorum* and *E. pinetorum* and ex-neotype of *Citromyces fuscus*	KM189547	KM088785	KM089557	KM089170
	DTO 097-F1 = CBS 235.60 = ATCC 18483 = QM 8040	Forest soil; Russia; ex-type of *P. silvaticum*	KM189568	KM088811	KM089583	KM089196
	DTO 006-I4 = CBS 139.72	Soil; Alaska, USA	KM189452	KM088676	KM089448	KM089061
	DTO 096-I5 = CBS 311.63	Forest soil; Netherlands	KM189567	KM088809	KM089581	KM089194
	DTO 181-H5 = CV 531 = KAS 4147 = DAOM 241356	Fynbos soil; Stellenbosch, South Africa	KM189652	KM088896	KM089670	KM089283
	DTO 202-C9 = CBS 129393 = WSF 15-C	Soil; A1 horizon Soil; Wisconsin conifer-hardwood forests, mixed forest; Wisconsin; USA	KM189724	KM088973	KM089747	KM089360
	DTO 205-H9 = CBS 129541 = RMF 8868	Soil; A1 horizon Soil; 40 yr old eastern white pine plantation, conifer forest, plantation; Coweeta Long-term Ecological Research (LTER) site; near Otto; North Carolina; USA	KM189730	KM088979	KM089753	KM089366
	DTO 208-D6 = CBS 129806 = RMF 7991,GW 4-4	Soil; lodgepole pine forest, conifer forest; Yellowstone National Park; Wyoming; USA	KM189737	KM088986	KM089760	KM089373
	DTO 209-A9 = CBS 130039 = RMF 7778	Soil; A1 horizon Soil; lodgepole pine forest, conifer forest; adjacent to Cinnabar Park; Medicine Bow National Forest; Wyoming; USA	KM189743	KM088992	KM089766	KM089379
	DTO 209-F6 = CBS 130199 = RMF 201	Soil; A1 horizon Soil; lodgepole pine forest, conifer forest; T16N R81W S28; west slope of Snowy Range; Wyoming; USA	KM189748	KM088997	KM089771	KM089384
	DTO 290-I7 = CBS 138.72	Soil; Alaska, USA	KM189778	KM089028	KM089802	KM089415
P. fusisporum	DTO 228-I3 = CBS 137778	*Protea roupelliae* var. *roupelliae*; Buffelskloof, South Africa	KM189757	KM089006	KM089780	KM089393
P. glabrum	DTO 279-F2 = CBS 138433 = NRRL 766	Unrecorded source; Unknown; ex-neotype of *P. aurantiobrunneum*	KM189775	KM089025	KM089799	KM089412
	DTO 076-G8 = CBS 125543 = IMI 91944 = IBT 22658 = DAOM 227653	Unrecorded source; ex-neotype of *P. glabrum*	KM189530	KM088767	KM089539	KM089152
	DTO 265-A9 = CBS 171.81 = IJFM 5072 = IMI 253790 = VKM F-2186	Culture contaminant of CBS 171.81; Utrecht, the Netherlands; ex-type of *P. aragonense*	KM189767	KM089017	KM089791	KM089404
	DTO 301-I3 = CBS 260.29 = IMI 092242 = LSHB P79 = MUCL 28650 = MUCL 29119 = NRRL 774	Unrecorded source; Belgium; ex-type of *P. flavidorsum*	KM189798	KM089048	KM089822	KM089435
	DTO 301-H8 = CBS 213.28 = FRR 770 = IMI 092265 = IMI 092265ii = LSHB P89 = MUCL 29118 = NRRL 770	Soil under conifer ; Tatry Mountains, Poland; ex-type of *P. oledzkii*	KM189795	KM089045	KM089819	KM089432
	DTO 301-I9 = CBS 344.59 = ATCC 18486 = IFO 5359 = IMI 068617 = NRRL 3460 = QM 8152	Butter; Japan; ex-type of *P. spinuloramigenum*	KM189803	KM089053	KM089827	KM089440
	DTO 301-I1 = CBS 228.28 = ATHUM 2896 = FRR 752 = IMI 092232 = LSHB P63 = MUCL 29114 = NRRL 752	Soil under conifer ; Poznan area, Poland; ex-type of *P. terlikowskii*	KM189797	KM089047	KM089821	KM089434
	DTO 005-G6	Cork; Portugal	KM189447	KM088671	KM089443	KM089056
	DTO 012-D5	Wood; Unknown	KM189453	KM088678	KM089450	KM089063

(*continued on next page*)

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. glabrum	DTO 015-I6	Soil; Los Alerces National Park, Chubut, Argentina	KM189454	KM088681	KM089453	KM089066
	DTO 015-I7	Soil; Los Alerces National Park, Chubut, Argentina	KM189455	KM088682	KM089454	KM089067
	DTO 015-I9	Soil; Los Alerces National Park, Chubut, Argentina	KM189456	KM088683	KM089455	KM089068
	DTO 016-A5	Soil; Puerto Piramides, Valdez peninsula, Chubet, Argentina	KM189457	KM088684	KM089456	KM089069
	DTO 036-B5 = CBS 171.81 = IJFM 5072 = IMI 253790 = VKM F-2186	Air; Madrid, Spain	KM189468	KM088700	KM089472	KM089085
	DTO 039-F6 = CBS 115810	Indoor environment; Germany	KM189477	KM088712	KM089484	KM089097
	DTO 056-H9 = FRR 6092	Living leaf of *Leptospermum polygofolium*; Collaroy, NSW, Australia	KM189500	KM088737	KM089509	KM089122
	DTO 056-I1 = FRR 6093	Bark of *Banksia ericifolia*; Lane Cove National Park, NSW, Australia	KM189501	KM088738	KM089510	KM089123
	DTO 056-I2 = FRR 6094	Living leaf of *Acacia suaveolans*; Collaroy, NSW, Australia	KM189502	KM088739	KM089511	KM089124
	DTO 057-A4 = FRR 6095	Litter under *Banksia integrifolia*; Collaroy, NSW, Australia	KM189513	KM088750	KM089522	KM089135
	DTO 057-A5 = FRR 6096	Soil; Roadside near Lockhart, NSW, Australia	KM189514	KM088751	KM089523	KM089136
	DTO 057-A7 = FRR 6097	Tree root; Katandra Nature Reserve, NSW, Australia	KM189515	KM088752	KM089524	KM089137
	DTO 057-B1 = FRR 6098	Soil, Eucalyptus forest; near Hamilton, Tas, Australia	KM189516	KM088753	KM089525	KM089138
	DTO 057-B3 = FRR 6099	Living leaf of *Leptospermum polygofolium*; Collaroy, NSW, Australia	KM189517	KM088754	KM089526	KM089139
	DTO 057-B4 = FRR 6100	From highly disturbed soil under Banksia integrifolia; School grounds, Terrigal, NSW, Australia	KM189518	KM088755	KM089527	KM089140
	DTO 067-E8	Cork; Portugal	KM189520	KM088757	KM089529	KM089142
	DTO 067-F2	Cork; Portugal	KM189521	KM088758	KM089530	KM089143
	DTO 067-F4	Cork; Portugal	KM189522	KM088759	KM089531	KM089144
	DTO 084-F6 = CBS 127704	Cork; Portugal	KM189533	KM088771	KM089543	KM089156
	DTO 084-F7 = CBS 127703	Cork; Portugal	KM189534	KM088772	KM089544	KM089157
	DTO 084-G2 = CBS 126333	Cork; Portugal	KM189536	KM088774	KM089546	KM089159
	DTO 084-G3 = CBS 126336	Cork; Portugal	KM189537	KM088775	KM089547	KM089160
	DTO 084-G7 = CBS 127700	Cork; Portugal	KM189540	KM088778	KM089550	KM089163
	DTO 085-B1 = CBS 138164	Soil, 2 mtr. from road; Ranoma fana, Madagascar	KM189544	KM088782	KM089554	KM089167
	DTO 087-H6 = CBS 138165	Swab sample taken in warehouse for fruits; the Netherlands	KM189546	KM088784	KM089556	KM089169
	DTO 099-A6	Soil in oak forest, taken at 0–10 cm depth; Aîn Hamraia, Tunesia	KM189571	KM088814	KM089586	KM089199
	DTO 119-E6	Soil in oak forest, taken at 10–20 cm depth; Fej Errih, Tunesia	KM189594	KM088838	KM089612	KM089225
	DTO 121-B6	Soil in oak forest, taken at 0–10 cm depth; Ras Rajel, Tunesia	KM189603	KM088847	KM089621	KM089234
	DTO 121-D9	Soil in oak forest, taken at 10–20 cm depth; Ras Rajel, Tunesia	KM189604	KM088848	KM089622	KM089235
	DTO 123-G9	Inside of chestnut; the Netherlands	KM189605	KM088849	KM089623	KM089236
	DTO 134-B4 = CBS 138166	Stone inside nectarine; the Netherlands	KM189611	KM088855	KM089629	KM089242
	DTO 153-H2	Cork; Algeria	KM189612	KM088856	KM089630	KM089243
	DTO 153-H4	Cork; Algeria	KM189613	KM088857	KM089631	KM089244
	DTO 153-H7	Cork; Algeria	KM189614	KM088858	KM089632	KM089245
	DTO 154-A1	Cork; Algeria	KM189615	KM088859	KM089633	KM089246
	DTO 154-F2	Cork; Algeria	KM189616	KM088860	KM089634	KM089247
	DTO 154-H3	Cork; Algeria	KM189617	KM088861	KM089635	KM089248
	DTO 155-C8	Cork; Algeria	KM189618	KM088862	KM089636	KM089249
	DTO 174-A1	Leaf of *Eucryphia cordifolia*; Tasmania, Australia	KM189619	KM088863	KM089637	KM089250

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. glabrum	DTO 174-A3	Leaf of *Eucalyptus* sp.; Lavers hill, Tasmania, Australia	KM189621	KM088865	KM089639	KM089252
	DTO 174-A7	Leaf of *Eucalyptus ovata*; Snake Gully, Kangaroo Island, Australia	KM189622	KM088866	KM089640	KM089253
	DTO 174-D7	Leaf of *Eucalyptus viminalis*; Kangaroo Island, Australia	KM189624	KM088868	KM089642	KM089255
	DTO 174-D9	Leaf of *Eucalyptus* sp.; Kangaroo Island, Australia	KM189626	KM088870	KM089644	KM089257
	DTO 178-I9 = KAS 3838	House dust; Stellenbosch, South Africa	KM189631	KM088875	KM089649	KM089262
	DTO 180-F8 = CV 4 = KAS 4125 = DAOM 241361	Air sample; Stellenbosch, South Africa	KM189639	KM088883	KM089657	KM089270
	DTO 181-C4 = CV 188 = KAS 4054 = DAOM 241132	*Protea repens* infructescence bract; Stellenbosch, South Africa	KM189647	KM088891	KM089665	KM089278
	DTO 182-H6 = CV 1181 = KAS 3980 = DAOM 241365	Mite inside *Protea repens* infructescence; Riverlands, South Africa	KM189677	KM088922	KM089696	KM089309
	DTO 183-B7 = CV 1494 = KAS 4015 = DAOM 241364	*Protea repens* infructescence bract; Riverlands, South Africa	KM189683	KM088929	KM089703	KM089316
	DTO 189-H9	Soil ; Spanderswoud, the Netherlands	KM189694	KM088941	KM089715	KM089328
	DTO 197-F9	Air sample; Bakery, Tilburg, The Netherlands	KM189718	KM088966	KM089740	KM089353
	DTO 203-I4	Soil; Aspear Island, Iran	KM189726	KM088975	KM089749	KM089362
	DTO 206-B4 = CBS 129602 = RMF 9521	Soil; Iraq	KM189732	KM088981	KM089755	KM089368
	DTO 206-B6 = CBS 129606 = RMF 9242	Soil; A1 horizon Soil; maple woods, deciduous forest; Cedar Creek Long-term Ecological Research (LTER) site; near East Bethel; Minnesota; USA	KM189733	KM088982	KM089756	KM089369
	DTO 208-B4 = CBS 129784 = RMF 8573 = RMF 8026	Soil; A1 horizon Soil; tallgrass prairie, grassland; Konza Prairie Research Natural Area; Long-term Ecological Research site (LTER); near Manhattan; Kansas; USA	KM189736	KM088985	KM089759	KM089372
	DTO 259-C6	Pile of moss; Eindhoven, the Netherlands	KM189764	KM089013	KM089787	KM089400
	DTO 262-G8	Soft drink; the Netherlands	KM189765	KM089014	KM089788	KM089401
	DTO 266-A8	Grapevine; Maragheh, Iran	KM189770	KM089020	KM089794	KM089407
	DTO 269-E1	House dust; South Africa	KM189771	KM089021	KM089795	KM089408
	DTO 296-H5 = CBS 131040 = RMF WT 97	Soil; Near Zurich; Switzerland	KM189785	KM089035	KM089809	KM089422
	DTO 297-D1 = CBS 328.48 = ATCC 10444 = IMI 040234 = LSHB Ad6 = NRRL 1915 = QM 1924	Unrecorded source	KM189790	KM089040	KM089814	KM089427
P. grancanariae	DTO 076-F3 = CBS 687.77 = IJFM 3745 = IMI 253783	Air; Canary Islands, Gran Canaria, Spain; ex-type of *P. grancanariae*	KM189529	KM088766	KM089538	KM089151
P. grevilleicola	DTO 174-E6 = CBS 137775	Leaf of Grevillea ilicifolia; Kingscote, Kangaroo Island; Australia; ex-type of *P. grevilleicola*	KM189630	KM088874	KM089648	KM089261
	DTO 174-E4	Leaf of *Grevillea ilicifolia*; Kingscote, Kangaroo Island; Australia	KM189629	KM088873	KM089647	KM089260
P. hoeksii	DTO 192-H4 = CBS 137776	Soil under Compact Rush (Juncus conglomeratus); De Ronde Put, Postel, Belgium; ex-type of *P. hoeksii*	KM189707	KM088954	KM089728	KM089341
	DTO 068-D9 = CBS 137952	Air in factory; Goes, the Netherlands	KM189523	KM088760	KM089532	KM089145
P. infra-aurantiacum	DTO 183-C3 = CBS 137747 = CV 1518 = KAS 4022 = DAOM 241145	Bracts of Protea repens infructescens; Riverlands, Malmesbury, Western Cape, South Africa; ex-type of *P. infra-aurantiacum*	KM189684	KM088930	KM089704	KM089317
	DTO 181-F1 = CBS 137746 = CV 362 = KAS 4118 = DAOM 241146	*Protea repens* infructescens; Stellenbosch mountain, Western Cape, South Africa	KM189650	KM088894	KM089668	KM089281
P. jejuense	DTO 174-D3 = CBS 137774	Leaf of *Eucalyptus* sp.; Lavers hill, Tasmania, Australia	KM189623	KM088867	KM089641	KM089254
	DTO 182-H7 = CBS 137755 = CV 1189 = KAS 3981 = DAOM 241142	Mite inside *Protea repens* infructescens; Riverlands, Malmesbury, Western Cape, South Africa	KM189678	KM088923	KM089697	KM089310

(*continued on next page*)

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. kananaskense	DTO 296-G7 = CBS 530.93 = ATCC 90282 = DAOM 216105 = IBT 11775 = IMI 356791	Soil, FH horizon, in a Pinus contorta var. latifolia forest; Kananaskis Valley, Alberta, Canada; ex-type of *P. kananaskense*	KM189780	KM089030	KM089804	KM089417
	DTO 193-A3	Moses under *Myrica gale* (Bog Myrtle); De Ronde Put, Postel, Belgium	KM189710	KM088957	KM089731	KM089344
P. kiamaense	DTO 056-I6 = CBS 137947 = FRR 6087	Soil; Barren Grounds National Park, NSW, Australia; ex-type of *P. kiamaense*	KM189506	KM088743	KM089515	KM089128
P. lividum	DTO 105-H6 = CBS 347.48 = ATCC 14941 = FRR 3407 = IFO 7740 = IHEM 4375 = IMI 099468 = MUCL 31326 = NRRL 3407 = DAOM 226266	Unrecorded source; Scotland; ex-neotype of *P. lividum*	KM189582	KM088825	KM089598	KM089211
	DTO 006-H8 = CBS 287.65	Litter of *Quercus* sp.; Lancashire, Grange-over-Sands, Merlewood Res. Station, UK	KM189450	KM088674	KM089446	KM089059
	DTO 198-I2 = CBS 128415 = WSF 3528	Soil; amorphus peat; above water table; cedar-fir forests, wetland, conifer forest; Wisconsin; USA	KM189720	KM088968	KM089742	KM089355
	DTO 297-D8 = CBS 132166 = WSF 3895	Soil; Wisconsin; USA	KM189794	KM089044	KM089818	KM089431
P. longicatenatum	DTO 180-D9 = CBS 137735 = CV 2847 = KAS 3943 = DAOM 241119	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa; ex-type of *P. longicatenatum*	KM189636	KM088880	KM089654	KM089267
	DTO 099-C6	Soil in oak forest, taken at 10–20 cm depth; Aîn Hamraia, Tunesia	KM189573	KM088816	KM089588	KM089201
	DTO 120-H9	Soil in oak forest, taken at 0–10 cm depth; Ras Rajel, Tunesia	KM189601	KM088845	KM089619	KM089232
	DTO 174-D8	Leaf of *Dodonea* sp.; Australia	KM189625	KM088869	KM089643	KM089256
	DTO 174-E2	Fruiting body on leaf of unknown sp; Kangaroo Island, Australia	KM189627	KM088871	KM089645	KM089258
	DTO 174-E3	Fruiting body on leaf of unknown sp; Kangaroo Island, Australia	KM189628	KM088872	KM089646	KM089259
	DTO 180-C8 = CBS 137742 = CV 2829 = KAS 3957 = DAOM 241120	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189633	KM088877	KM089651	KM089264
	DTO 180-D2 = CBS 137734 = CV 2840 = KAS 3935 = DAOM 241118	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189634	KM088878	KM089652	KM089265
	DTO 180-D6CV 2843 = KAS 3940	Fynbos soil; Riverlands, South Africa	KM189635	KM088879	KM089653	KM089266
	DTO 181-C7 = CBS 137737 = CV 209 = KAS 4069 = DAOM 241122	Mite inside *Protea repens* infructescens; Stellenbosch mountain, Western Cape, South Africa	KM189648	KM088892	KM089666	KM089279
	DTO 181-C8 = CV 214 = KAS 4070	*Protea repens* infructescence bract; Stellenbosch, South Africa	KM189649	KM088893	KM089667	KM089280
	DTO 182-B8 = CBS 137738 = CV 885 = KAS 4188 = DAOM 241149	Soil from Fynbos; Stellenbosch mountain, Western Cape, South Africa	KM189658	KM088902	KM089676	KM089289
	DTO 182-G2 = CV 997 = KAS 4231	Mite inside Protea repens infructescence; Riverlands, South Africa	KM189672	KM088917	KM089691	KM089304
	DTO 182-G6 = CBS 137739 = CV 1036 = KAS 3964 = DAOM 241148	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189673	KM088918	KM089692	KM089305
	DTO 182-I9 = CBS 137740 = CV 1300 = KAS 3995 = DAOM 241123	*Protea repens* infructescens; Riverlands, Malmesbury, Western Cape, South Africa	KM189679	KM088925	KM089699	KM089312
	DTO 183-A1 = CV 1301 = KAS 3996	*Protea repens* infructescence bract; Riverlands, South Africa	KM189680	KM088926	KM089700	KM089313
	DTO 183-A3 = CBS 137741 = CV 1335 = KAS 3999 = DAOM 241147	Soil from Fynbos; Riverlands, Malmesbury, Western Cape, South Africa	KM189681	KM088927	KM089701	KM089314
	DTO 183-C6 = CV 1585 = KAS 4025	*Protea repens* infructescence bract; Riverlands, South Africa	KM189685	KM088931	KM089705	KM089318
	DTO 216-B6	Foliar tissue of *Populus angustifolia*; Ogden, UT, USA	KM189751	KM089000	KM089774	KM089387
P. malmesburiense	DTO 182-H5 = CBS 137744 = CV 1180 = KAS 3979 = DAOM 241144	Mite inside Protea repens infructescens; Riverlands, Malmesbury, Western Cape, South Africa; ex-type of *P. malmesburiense*	KM189676	KM088921	KM089695	KM089308

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. malmesburiense	DTO 183-A6 = CBS 137745 = CV 1422 = KAS 4003 = DAOM 241143	*Protea repens* infructescens; Riverlands, Malmesbury, Western Cape, South Africa	KM189682	KM088928	KM089702	KM089315
P. montanense	DTO 090-I6 = CBS 310.63 = ATCC 14941 = FRR 3407 = IFO 7740 = IHEM 4375 = IMI 099468 = MUCL 31326 = NRRL 3407 = DAOM 226282	Coniferous forest soil; Ravalli Co., Montana, USA; ex-type of *P. montanense*	KM189551	KM088789	KM089561	KM089174
	DTO 041-D7	Soil; Poland	KM189482	KM088718	KM089490	KM089103
	DTO 196-B6 = CBS 126808 = WSF 2021	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA	KM189713	KM088961	KM089735	KM089348
	DTO 196-D2 = CBS 126824 = WSF 3733 = WSF 2021	Soil; amorphus peat; above water table; cedar-fir forests, wetland, conifer forest; Wisconsin; USA	KM189714	KM088962	KM089736	KM089349
	DTO 196-D4 = CBS 126826 = WSF 3952	Soil; amorphus peat; above water table; open bogs, wetland, shrubland; Wisconsin; USA	KM189715	KM088963	KM089737	KM089350
	DTO 196-E1 = CBS 126832 = WSF 3124	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA	KM189716	KM088964	KM089738	KM089351
	DTO 196-E2 = CBS 126833	Culture contaminant of WSF 2127	KM189717	KM088965	KM089739	KM089352
	DTO 198-I4 = CBS 128418 = WSF 3450	Soil; amorphus peat; above water table; cedar-fir forests, wetland, conifer forest; Wisconsin; USA	KM189721	KM088969	KM089743	KM089356
	DTO 198-I6 = CBS 128426 = WSF 3315	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA	KM189722	KM088970	KM089744	KM089357
	DTO 208-F3 = CBS 129881 = RMF 8750	Soil; A1 horizon Soil; coniferous forest ecosystem, conifer forest; Andrews Long-term Ecological Research (LTER) site; Willamette National Forest; near Blue River; Oregon; USA	KM189740	KM088989	KM089763	KM089376
	DTO 208-I7 = CBS 130027 = RMF 7785	Soil; A1 horizon Soil; lodgepole pine forest, conifer forest; adjacent to Cinnabar Park; Medicine Bow National Forest; Wyoming; USA	KM189742	KM088991	KM089765	KM089378
	DTO 209-F4 = CBS 130197 = RMF 199	Soil; A1 horizon Soil; lodgepole pine forest, conifer forest; T16N R81W S28; west slope of Snowy Range; Wyoming; USA	KM189747	KM088996	KM089770	KM089383
	DTO 209-F9 = CBS 130202 = RMF 204	Soil; A1 horizon Soil; lodgepole pine forest, conifer forest; T16N R81W S28; west slope of Snowy Range; Wyoming; USA	KM189749	KM088998	KM089772	KM089385
	DTO 263-I9	*Pseudotsuga menziesii* var. *glauca*; White Pass, Cascade Mts. Washington, USA	KM189766	KM089015	KM089789	KM089402
P. odoratum	DTO 290-I9 = CBS 432.65 = FAT 1138 = IFO 6039	Soil ; Japan; ex-syntype of *P. trzebinskianum*	KM189779	KM089029	KM089803	KM089416
	DTO 205-B7 = CBS 294.62 = CBS 129423 = WSF 2000 = DAOM 226269 = ATCC 14769 = DSM 2419 = IFO 7741 = IMI 094208ii = NRRL 3007 = DAOM 226269	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA; ex-type of *P. odoratum*	KM189727	KM088976	KM089750	KM089363
	DTO 296-H8 = CBS 431.65 = FAT 728 = IAM 7193 = IFO 6038	Soil; Japan; ex-type of *P. trzebinskianum*	KM189788	KM089038	KM089812	KM089425
	DTO 198-H8 = CBS 128282 = WSF 3201	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA	KM189719	KM088967	KM089741	KM089354
	DTO 201-B2 = CBS 128274 = WSF 3200	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA	KM189723	KM088972	KM089746	KM089359
	DTO 205-C5 = CBS 129440 = WSF 2002	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA	KM189728	KM088977	KM089751	KM089364

(*continued on next page*)

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. odoratum	DTO 206-B7 = CBS 129607 = RMF 9241	Soil; A1 horizon soil; maple woods, deciduous forest; Cedar Creek Long-term Ecological Research (LTER) site; near East Bethel; Minnesota; USA	KM189734	KM088983	KM089757	KM089370
	DTO 208-E5 = CBS 129874 = RMF 8759	Soil; A1 horizon soil; coniferous forest ecosystem, conifer forest; Andrews Long-term Ecological Research (LTER) site; Willamette National Forest; near Blue River; Oregon; USA	KM189739	KM088988	KM089762	KM089375
	DTO 296-H7 = CBS 129135 = WSF 3894	Soil; Wisconsin; USA	KM189787	KM089037	KM089811	KM089424
	DTO 301-H9 = CBS 217.30 = NRRL 2062	Unrecorded source	KM189796	KM089046	KM089820	KM089433
P. palmense	DTO 076-E2 = CBS 336.79 = ATCC 38669 = IJFM 3840 = VKM F-2181	Air; Canary Islands, Gran Canaria, Spain; ex-type of *P. palmense*	KM189528	KM088765	KM089537	KM089150
P. pulvis	DTO 180-B7 = CBS 138432 = KAS 3924	House dust; South Africa; ex-type of *P. pulvis*	KM189632	KM088876	KM089650	KM089263
	DTO 180-F9 = CV 7 = KAS 4166 = DAOM 241133	Air sample; Stellenbosch, South Africa	KM189640	KM088884	KM089658	KM089271
	DTO 180-G2 = CV 15 = KAS 4017 = DAOM 241135	Air sample; Stellenbosch, South Africa	KM189641	KM088885	KM089659	KM089272
P. purpurescens	DTO 091-D2 = CBS 366.48 = ATCC 10485 = IMI 039745 = NRRL 720 = QM 1959	Soil; Canada; ex-neotype of *P. purpurescens*	KM189561	KM088801	KM089573	KM089186
	DTO 091-D3 = CBS 126.64	Soil; Erzurum, Turkey	KM189562	KM088802	KM089574	KM089187
P. quercetorum	DTO 091-A5 = CBS 417.69 = ATCC 48727 = CCRC 31668 = FRR 516 = IFO 31749 = IMI 140342 = MUCL 31203 = VKM F-1074	Soil; Es-Euveida, Syria; ex-isotype of *P. quercetorum*	KM189556	KM088795	KM089567	KM089180
	DTO 208-D9 = CBS 129869 = RMF 8789	Soil; A1 horizon soil; coniferous forest ecosystem, conifer forest; Andrews Long-term Ecological Research (LTER) site; Willamette National Forest; near Blue River; Oregon; USA	KM189738	KM088987	KM089761	KM089374
P. ranomafanaense	DTO 085-A5 = CBS 137953	Soil, 2 mtr. from road; Ranoma fana, Madagascar; ex-type of *P. ranomafanaense*	KM189541	KM088779	KM089551	KM089164
	DTO 085-A8 = CBS 137954	Soil, 2 mtr. from road; Ranoma fana, Madagascar	KM189543	KM088781	KM089553	KM089166
P. roseomaculatum	DTO 290-I6 = CBS 137254 = IMI 92236	Unrecorded source; ex-type of *P. baiiolum*	KM189777	KM089027	KM089801	KM089414
	DTO 225-E3 = CBS 137962 = NRRL 728 = FRR 0728 = IMI 189696 = MUCL 29101	Unrecorded source; ex-type of *P. roseomaculatum*	KM189755	KM089004	KM089778	KM089391
	DTO 084-F8 = CBS 125096	Cork; Portugal; ex-type of *P. subericola*	KM189535	KM088773	KM089545	KM089158
	DTO 035-A1 = CBS 137944	Soil; New Zealand	KM189465	KM088697	KM089469	KM089082
	DTO 035-A3	Soil; New Zealand	KM189466	KM088698	KM089470	KM089083
	DTO 053-F7 = CBS 125097 = IBT 23009	Air; Vejle, Denmark	KM189490	KM088727	KM089499	KM089112
	DTO 057-A2 = CBS 125100 = FRR 4914	Dried grapes (sultanas) (*Vitis vinifera*); Mildura, Vic, Australia	KM189511	KM088748	KM089520	KM089133
	DTO 098-E2 = CBS 127706 = KAS 1289	Lumber; BC, Vancouver, Canada	KM189570	KM088813	KM089585	KM089198
	DTO 100-A7 = CBS 125099 = IBT 20217	Acified lake; Butte, Montana, USA	KM189579	KM088822	KM089595	KM089208
	DTO 100-A8 = CBS 125098 = IBT 20218	Acified lake; Butte, Montana, USA	KM189580	KM088823	KM089596	KM089209
P. roseoviride	DTO 090-I2 = CBS 267.35 = ATCC 10412 = IFO 6089 = IMI 039740ii = NRRL 760 = QM 7485	Soil in a beech forest; Germany; ex-type of *P. roseoviride*	KM189549	KM088787	KM089559	KM089172
P. rudallense	DTO 209-C1 = CBS 130049 = RMF 7766	Soil (beehives); USA; ex-type of *P. rudallense*	KM189744	KM088993	KM089767	KM089380
	DTO 030-G5	Soil; Barron falls, Queensland, Australia	KM189463	KM088692	KM089464	KM089077
	DTO 056-I4 = CBS 138162 = FRR 6085	Soil; Rudall River National Park, WA, Australia	KM189504	KM088741	KM089513	KM089126
	DTO 057-B5 = FRR 6091	Soil; Rudall River National Park, WA, Australia	KM189519	KM088756	KM089528	KM089141
	DTO 180-G4 = CBS 138558 = CV 26 = KAS 4104 = DAOM 241136	Air sample; Stellenbosch, South Africa	KM189638	KM088882	KM089656	KM089269

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. saturniforme	DTO 105-I8 = CBS 122276 = AS 3.6886 = HMAS 130355-1-4	Soil; Little Peony Forest Reserve, Dunhua, Jiling Province, China ; ex-type of *E. saturniforme*	KM189585	KM088828	KM089601	KM089214
Penicillium sp.	DTO 181-I3 = CBS 137729 = CV 550 = KAS 4156 = DAOM 241129	Soil from Fynbos; Stellenbosch mountain, Western Cape, South Africa	KM189654	KM088898	KM089672	KM089285
P. spinulosum	DTO 006-H1 = CBS 374.48 = ATCC 10498 = FRR 1750 = IMI 024316 = MUCL 13910 = MUCL 13911 = NCTC 591 = NRRL 1750 = QM 7654 = DAOM 226267	Culture contaminant; Hannover, Germany; ex-neotype of *P. spinulosum*	KM189448	KM088672	KM089444	KM089057
	DTO 296-G8 = CBS 348.59 = ATCC 22346 = FAT 24 = FRR 3406 = IFO 6239 = IMI 068222 = MUCL 13555 = NRRL 3406 = DAOM 226268	Soil; Ukaku, Japan; ex-type of *P. abeanum* and *P. trzebinskii* var. *magnum*	KM189781	KM089031	KM089805	KM089418
	DTO 279-F1 = CBS 137964 = NRRL 2051	Unrecorded source; ex-type of *P. flavocinereum*	KM189774	KM089024	KM089798	KM089411
	DTO 301-I5 = CBS 269.35	Forest litter; Germany; ex-type of *P. mucosum*	KM189800	KM089050	KM089824	KM089437
	DTO 301-I6 = CBS 271.35	Forest leaf litter; Germany; ex-type of *P. tannophilum*	KM189801	KM089051	KM089825	KM089438
	DTO 290-I3 = CBS 137257 = IMI 190575	Unrecorded source; Probably ex-type of *P. brunneoviride* (Pitt 1980: 180)	KM189776	KM089026	KM089800	KM089413
	DTO 279-E9 = CBS 137963 = NRRL 727	Unrecorded source; Representative of *P. pfefferianum*	KM189773	KM089023	KM089797	KM089410
	DTO 056-I8 = CBS 137948	Bark of *Banksia ericifolia*; Lane Cove National Park, NSW, Australia	KM189508	KM088745	KM089517	KM089130
	DTO 084-G5 = CBS 127698	Cork; Portugal	KM189538	KM088776	KM089548	KM089161
	DTO 084-G6 = CBS 127699	Cork; Portugal	KM189539	KM088777	KM089549	KM089162
P. sterculiniicola	DTO 031-A4 = CBS 122426	Spawn run compost; USA; ex-type of *P. sterculiniicola*	KM189464	KM088693	KM089465	KM089078
	DTO 004-B8 = CBS 117778	Potting soil; the Netherlands	KM189446	KM088670	KM089442	KM089055
	DTO 035-A4	Soil; New Zealand	KM189467	KM088699	KM089471	KM089084
	DTO 216-I4 = CBS 137960	Root tissue of *Pinus ponderosa*; University of Idaho greenhouse, USA	KM189753	KM089002	KM089776	KM089389
	DTO 216-I8 = CBS 137961	Root tissue of *Pinus ponderosa*; University of Idaho greenhouse, USA	KM189754	KM089003	KM089777	KM089390
P. sublectaticum	DTO 076-C5 = CBS 138163	Unknown marine source; New Zealand; ex-type of *P. sublectaticum*	KM189527	KM088764	KM089536	KM089149
	DTO 244-G2 = CBS 138217	House dust; New Zealand	KM189761	KM089010	KM089784	KM089397
P. subspinulosum	DTO 018-C8	Log of *Pinus* sp.; Spanderswoud, Bussum, the Netherlands	KM189459	KM088686	KM089458	KM089071
	DTO 038-G1	Forest soil; Rijnsweerd, Utrecht, the Netherlands	KM189476	KM088711	KM089483	KM089096
	DTO 040-E6	Soil; Poland	KM189478	KM088713	KM089485	KM089098
	DTO 041-F2 = CBS 137946	Soil; Poland	KM189483	KM088719	KM089491	KM089104
	DTO 042-F7	Soil; Poland	KM189484	KM088720	KM089492	KM089105
	DTO 056-I9 = CBS 137949 = FRR 4882	Roots of Wollemi Pine (*Wollemia nobilis*); Wollemi National Park, NSW, Australia	KM189509	KM088746	KM089518	KM089131
	DTO 057-A1 = CBS 137950 = FRR 4872	Roots of Wollemi Pine (*Wollemia nobilis*); Wollemi National Park, NSW, Australia	KM189510	KM088747	KM089519	KM089132
	DTO 057-A3 = CBS 137951 = FRR 6090	Soil; Barren Grounds National Park, NSW, Australia	KM189512	KM088749	KM089521	KM089134
	DTO 092-G4 = CBS 137955	Soil under Betula sp.; Cartier Heide, Eersel, the Netherlands	KM189563	KM088803	KM089575	KM089188
	DTO 189-H2	Soil; Spanderswoud, the Netherlands	KM189693	KM088940	KM089714	KM089327
	DTO 189-I3	Soil; Spanderswoud, the Netherlands	KM189695	KM088942	KM089716	KM089329
	DTO 190-A1	Soil; Spanderswoud, the Netherlands	KM189696	KM088943	KM089717	KM089330
	DTO 190-C8	Soil; Spanderswoud, the Netherlands	KM189698	KM088945	KM089719	KM089332
	DTO 190-D2 = CBS 137957	Soil; Spanderswoud, the Netherlands	KM189699	KM088946	KM089720	KM089333
	DTO 190-D4	Soil; Spanderswoud, the Netherlands	KM189700	KM088947	KM089721	KM089334

(*continued on next page*)

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. subspinulosum	DTO 190-D5 = CBS 137958	Soil; Spanderswoud, the Netherlands	KM189701	KM088948	KM089722	KM089335
	DTO 190-D9	Soil; Spanderswoud, the Netherlands	KM189702	KM088949	KM089723	KM089336
	DTO 206-C4 = CBS 129613 = RMF 9368 = RMF 8940	Soil; A1 horizon Soil; abandoned agricultural fields; aged 1–10 years, agriculture; Cedar Creek Long-term Ecological Research (LTER) site; near East Bethel; Minnesota; USA	KM189735	KM088984	KM089758	KM089371
	DTO 208-H6 = CBS 129906 = RMF 8736	Soil; A1 horizon Soil; coniferous forest ecosystem, conifer forest; Andrews Long-term Ecological Research (LTER) site; Willamette National Forest; near Blue River; Oregon; USA	KM189741	KM088990	KM089764	KM089377
	DTO 296-H2 = CBS 345.51 = ATCC 11080 = IMI 046814 = NRRL 2298 = QM 6901 = UPSC 3182	Soil; England, UK	KM189783	KM089033	KM089807	KM089420
	DTO 297-D5 = CBS 290.53	Unrecorded source	KM189792	KM089042	KM089816	KM089429
	DTO 297-D6 = CBS 128281 = WSF 3202	Soil; Wisconsin; USA	KM189793	KM089043	KM089817	KM089430
P. thiersii	DTO 037-I9 = CBS 117503 = IBT 27050 = NRRL 28162	Old black stroma of Hypoxylon encrusting the surface of a dead maple ; New Glarus Woods State Park, Wisconsin, USA; ex-type of *P. thiersii*	KM189474	KM088709	KM089481	KM089094
P. thomii	DTO 091-A9 = CBS 225.81 = IMI 189694 = NRRL 2077	Pine cone; Spaulding, Georgia, USA; ex-neotype of *P. thomii*	KM189560	KM088799	KM089571	KM089184
	DTO 036-C3 = CBS 257.87 = FRR 2676	Dried fish, *Decapterus* sp.; Indonesia; ex-type of *P. corynephorum*	KM189469	KM088701	KM089473	KM089086
	DTO 105-I6 = CBS 260.87 = FRR 2662	Dried fish; *Rastrelliger kanagurta*, Indonesia; ex-type of *P. patens*	KM189584	KM088827	KM089600	KM089213
	DTO 202-E5 = CBS 129408 = WSF 2003	Soil; amorphus peat; above water table; spruce-larch forests, wetland, conifer forest; Wisconsin; USA	KM189725	KM088974	KM089748	KM089361
	DTO 205-H3 = CBS 129534 = RMF 8828	Soil; A1 horizon Soil; native deciduous forest, deciduous forest; Coweeta Long-term Ecological Research (LTER) site; near Otto; North Carolina; USA	KM189729	KM088978	KM089752	KM089365
P. trzebinskii	DTO 301-I4 = CBS 268.35	Forest litter; Germany; ex-type of *P. mediocre*	KM189799	KM089049	KM089823	KM089436
	DTO 301-I7 = CBS 289.36	Tannin solution; Germany; ex-type of *P. tannophagum*	KM189802	KM089052	KM089826	KM089439
	DTO 006-H2 = CBS 351.51	Rice; Japan; ex-type of *P. toxicarium*	KM189449	KM088673	KM089445	KM089058
	DTO 296-H3 = CBS 382.48 = ATCC 10507 = FRR 731 = IFO 6110 = IMI 039749 = MUCL 29102 = NRRL 731 = QM 7678	Forest soil; Dluga Goslina, Poznan area, Poland; ex-type of *P. trzebinskii*	KM189784	KM089034	KM089808	KM089421
	DTO 036-E1	Soil; Poland	KM189470	KM088703	KM089475	KM089088
	DTO 040-F3	Soil; Poland	KM189479	KM088714	KM089486	KM089099
	DTO 040-H8 = CBS 137945	Soil; Poland	KM189480	KM088716	KM089488	KM089101
	DTO 040-I8	Soil; Poland	KM189481	KM088717	KM089489	KM089102
	DTO 190-G2	Soil; Spanderswoud, the Netherlands	KM189703	KM088950	KM089724	KM089337
	DTO 209-D5 = CBS 130062 = RMF 7822	Soil; rhizosphere of onion; onion field, agriculture; University of Idaho Experiment Station; Parma; Idaho; USA	KM189745	KM088994	KM089768	KM089381
	DTO 297-D3 = CBS 128424 = WSF 3448	Soil; Wisconsin; USA	KM189791	KM089041	KM089815	KM089428
P. tsitsikammaense	DTO 006-I3 = CBS 328.71 = CSIR 1092	Forest soil; Tsitsikama Forest near Knysna, Cape Province, South-Africa	KM189451	KM088675	KM089447	KM089060
P. turcosoconidiatum	DTO 181-A3 = CBS 138557 = CV 110 = KAS 3970 = DAOM 241130	Fynbos soil; Stellenbosch, South Africa; ex-type of *P. turcosoconidiatum*	KM189645	KM088889	KM089663	KM089276
	DTO 181-A4 = CBS 137733 = CV 111 = KAS 3971 = DAOM 241131	Soil from Fynbos; Stellenbosch mountain, Western Cape, South Africa	KM189646	KM088890	KM089664	KM089277
P. vagum	DTO 180-G3 = CBS 137728 = CV 25 = KAS 4100 = DAOM 241357	Air sample from Fynbos; Stellenbosch mountain, Western Cape, South Africa; ex-type of *P. vagum*	KM189642	KM088886	KM089660	KM089273
	DTO 038-E7	Forest soil; Rijnsweerd, Utrecht, the Netherlands	KM189475	KM088710	KM089482	KM089095
	DTO 056-I3 = FRR 4783	Fresh currants (*Vitis vinifera*); Mildura, Vic, Australia	KM189503	KM088740	KM089512	KM089125

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. vagum	DTO 056-I5 = FRR 6086	Soil; Katandra Nature Reserve, NSW, Australia	KM189505	KM088742	KM089514	KM089127
	DTO 056-I7 = FRR 6088	Soil; Roadside north of Urana, NSW, Australia	KM189507	KM088744	KM089516	KM089129
	DTO 099-A7	Soil in oak forest, taken at 0–10 cm depth; Aîn Hamraia, Tunesia	KM189572	KM088815	KM089587	KM089200
	DTO 099-D6	Soil in oak forest, taken at 0–10 cm depth; Aîn Hamraia, Tunesia	KM189574	KM088817	KM089589	KM089202
	DTO 099-F7	Soil in oak forest, taken at 0–10 cm depth; Aîn Hamraia, Tunesia	KM189576	KM088819	KM089591	KM089204
	DTO 099-G7	Soil in oak forest, taken at 10–20 cm depth; Aîn Hamraia, Tunesia	KM189577	KM088820	KM089592	KM089205
	DTO 099-I6	Soil in oak forest, taken at 0–20 cm depth; Aîn Hamraia, Tunesia	KM189578	KM088821	KM089594	KM089207
	DTO 119-A8	Soil in oak forest, taken at 10–20 cm depth; Fej Errih, Tunesia	KM189588	KM088832	KM089606	KM089219
	DTO 119-C2	Soil in oak forest, taken at 0–10 cm depth; Fej Errih, Tunesia	KM189589	KM088833	KM089607	KM089220
	DTO 119-C8	Soil in oak forest, taken at 0–10 cm depth; Fej Errih, Tunesia	KM189590	KM088834	KM089608	KM089221
	DTO 119-D6	Soil in oak forest, taken at 10–20 cm depth; Fej Errih, Tunesia	KM189591	KM088835	KM089609	KM089222
	DTO 119-D7	Soil in oak forest, taken at 10–20 cm depth; Fej Errih, Tunesia	KM189592	KM088836	KM089610	KM089223
	DTO 119-E2	Soil in oak forest, taken at 10–20 cm depth; Fej Errih, Tunesia	KM189593	KM088837	KM089611	KM089224
	DTO 119-G4	Soil in oak forest, taken at 0–10 cm depth; Fej Errih, Tunesia	KM189595	KM088839	KM089613	KM089226
	DTO 119-H7	Soil in oak forest, taken at 0–20 cm depth; Ras Rajel, Tunesia	KM189596	KM088840	KM089614	KM089227
	DTO 120-B1	Soil in oak forest, taken at 0–20 cm depth; Ras Rajel, Tunesia	KM189597	KM088841	KM089615	KM089228
	DTO 120-B4	Soil in oak forest, taken at 0–20 cm depth; Ras Rajel, Tunesia	KM189598	KM088842	KM089616	KM089229
	DTO 120-C1	Soil in oak forest, taken at 0–20 cm depth; Ras Rajel, Tunesia	KM189599	KM088843	KM089617	KM089230
	DTO 120-C7	Soil in oak forest, taken at 0–20 cm depth; Ras Rajel, Tunesia	KM189600	KM088844	KM089618	KM089231
P. valentinum	DTO 090-I3 = CBS 172.81 = IJFM 5071	Air; Madrid, Spain; ex-type of *P. valentinum*	KM189550	KM088788	KM089560	KM089173
	DTO 091-A4 = CBS 381.48 = ATCC 10506 = DSM 2214 = IMI 040027 = NRRL 1640 = QM 8002	Air; Natick, Massachusetts, USA	KM189555	KM088794	KM089566	KM089179
	DTO 205-I6 = CBS 129547 = RMF 9020	Soil; A1 horizon Soil; oak savanna, savanna; Cedar Creek Long-term Ecological Research (LTER) site; near East Bethel; Minnesota; USA	KM189731	KM088980	KM089754	KM089367
	DTO 296-H6 = CBS 131033 = RMF 2158	Soil; Grand Teton National Park; T44N R113W S5&6; Wyoming; USA	KM189786	KM089036	KM089810	KM089423
P. verhagenii	DTO 193-A1 = CBS 137959	Moses under Myrica gale (Bog Myrtle); De Ronde Put, Postel, Belgium; ex-type of *P. verhagenii*	KM189708	KM088955	KM089729	KM089342
	DTO 023-E1 = CBS 146.83	Isolated from CBS 145.83 on a synthetic medium; Spain	KM189460	KM088688	KM089460	KM089073
	DTO 028-G1	Indoor air of house; Eindhoven, the Netherlands	KM189461	KM088689	KM089461	KM089074
	DTO 192-G4	Soil under Compact Rush (*Juncus conglomeratus*); De Ronde Put, Postel, Belgium	KM189704	KM088951	KM089725	KM089338
	DTO 192-G7	Soil under Compact Rush (*Juncus conglomeratus*); De Ronde Put, Postel, Belgium	KM189705	KM088952	KM089726	KM089339
	DTO 193-A2	Moses under *Myrica gale* (Bog Myrtle); De Ronde Put, Postel, Belgium	KM189709	KM088956	KM089730	KM089343
	DTO 193-A5	Moses under *Myrica gale* (Bog Myrtle); De Ronde Put, Postel, Belgium	KM189711	KM088958	KM089732	KM089345

(*continued on next page*)

Table 1. (Continued).

Species name	Collection no.	Substrate, location	GenBank accession nr.			
			ITS	*BenA*	*RPB2*	*CaM*
P. yezoense	DTO 091-A2 = CBS 350.59 = ATCC 18333 = FRR 3395 = IFO 5362 = IMI 068615	Butter; Japan; ex-type of *P. yezoense*	KM189553	KM088792	KM089564	KM089177
	DTO 001-G9 = CBS 117276	Soil; Alpujarras, Spain	KM189445	KM088669	KM089441	KM089054
	DTO 091-A7 = CBS 140.72	Soil; Alaska, USA	KM189558	KM088797	KM089569	KM089182
	DTO 091-A8 = CBS 347.78	Soil under *Picea glauca*, containing 400 ppm Ni and Cu; 29.3 km SE of Sudbury, Ontario, Canada	KM189559	KM088798	KM089570	KM089183
	DTO 099-E2	Soil in oak forest, taken at 10–20 cm depth; Aîn Hamraia, Tunesia	KM189575	KM088818	KM089590	KM089203
	DTO 118-E5	Soil in oak forest, taken at 0–20 cm depth; Fej Errih, Tunesia	KM189587	KM088831	KM089604	KM089217
	DTO 121-A4	Soil in oak forest, taken at 10–20 cm depth; Ras Rajel, Tunesia	KM189602	KM088846	KM089620	KM089233
	DTO 190-B7	Soil; Spanderswoud, the Netherlands	KM189697	KM088944	KM089718	KM089331
	DTO 192-G8	Soil under Compact Rush (*Juncus conglomeratus*); De Ronde Put, Postel, Belgium	KM189706	KM088953	KM089727	KM089340
	DTO 193-G2	Moses under *Myrica gale* (Bog Myrtle); De Ronde Put, Postel, Belgium	KM189712	KM088959	KM089733	KM089346
	DTO 209-F1 = CBS 130194 = RMF 157	Soil; A1 horizon Soil; narrowleaf cottonwood, deciduous forest; Fort Steele Road; 2 miles south of Interstate 80; 9 miles east of Sinclair; Wyoming; USA	KM189746	KM088995	KM089769	KM089382
	DTO 216-B7	Foliar tissue of *Populus trichocarpa*; Nisqually River, WA, USA	KM189752	KM089001	KM089775	KM089388
	DTO 270-H9	Air in nickelsulfate production facility; Belgium	KM189772	KM089022	KM089796	KM089409

and CYA supplemented with 5 % NaCl (Samson *et al.* 2010). Growth of the isolates was also examined on CYA at 15, 30 and 37 °C (CYA15°C, CYA30°C and CYA37°C, respectively). Strains were inoculated at three points onto media in 90 mm Petri dishes and incubated for 7 d in darkness. After incubation, colony diameters on each agar medium were measured. In addition, degree of sporulation, obverse and reverse colony colours, colony shape and texture, and the production of soluble pigments were determined. Acid production on CREA was indicated by a change in the pH sensitive bromocresole purple dye from purple to yellow around growing colonies. Colonies were photographed with a Canon EOS 400D. Species were characterised microscopically by preparing slides from MEA. Lactic acid was used as mounting fluid and a drop of alcohol was added to remove air bubbles and excess conidia. Specimens were examined using a Zeiss AxioSkop2 plus microscope. Strains were also examined for production of alkaloids reacting with Ehrlich reagent using a filter paper method (Lund 1995). The appearance of a violet ring within 10 min was regarded as a positive reaction; all other colours were considered as a negative reaction.

RESULTS AND DISCUSSION

Overview of section *Aspergilloides*

The phylogenetic relationships among species belonging to section *Aspergilloides* were studied using concatenated sequence data of three loci, *BenA*, *CaM* and *RPB2*. In total, 112 mostly ex-type strains were included in the analysis and the total length of the aligned data set was 2 049 characters. The length and the best substitution model for each partition are summarised in Table 2. Members of section *Aspergilloides* formed a well-supported lineage in the phylogram (100 % ML, 1.00 pp) and section *Sclerotiora* species form a sister clade to *Aspergilloides*, although with low statistical support (77 % ML, <0.95 pp). These results largely correspond with those of Houbraken & Samson (2011); however, there are two main differences. In Houbraken & Samson (2011), *Penicillium thiersii* CBS 117503 occupied a well-supported basal position in section *Aspergilloides* based on a combined analysis of four genes (*Cct8*, *Tsr1*, *RPB1* and *RPB2*). In our phylogeny, this species is basal to section *Aspergilloides* without statistical support. This species could represent a separate section close to sections *Aspergilloides* and *Sclerotiora*, but based on Houbraken & Samson (2011), we opt to provisionally maintain its classification in section *Aspergilloides*. The other difference is the placement of *P. georgiense* in section *Aspergilloides* (Houbraken & Samson 2011). Our data show that this species does not belong to this section and Fig. 1 indicates a relationship with *P. ramusculum* (CBS 251.56^{T}) in section *Ramigena*.

Fig. 1 reveals the presence of 12 well-supported lineages in section *Aspergilloides*. All lineages were fully supported (100 % ML, 1.00 pp) with exception of the *P. thiersii* (<70 % ML; <0.95 pp) and *P. vagum*-clades (81 % ML, 0.96 pp). All accepted species, except *P. kiamaense*, could be assigned to one of the delineated lineages. Bayesian analysis showed that this species is basal to the *P. spinulosum*- and *P. thomii*-clade (0.99 pp); however, this was not supported in the ML analysis. Most

Table 2. Overview details of sequence data sets used in this study.

Clade	Description data set	No. isolates	Data sets					
			BenA	**Substitution model**	***CaM***	**Substitution model**	***RPB2***	**Substitution model**
	Overview *Aspergilloides*	112	541	GTR+G+I	620	GTR+G+I	888	GTR+G+I
1	*P. spinulosum-clade*	73	438	K2+G	520	GTR+G	888	GTR+G+I
2	*P. thomii-clade*	43	439	HKY+G	527	GTR+G	764	GTR+G
3	*P. glabrum-clade*	104	438	K2P+G	501	GTR+G	887	GTR+G
4	*P. vagum-clade*	44	469	K2+G	524	K2+I	866	GTR+G
5	*P. fuscum-clade*	62	471	K2+G	527	GTR+G	755	GTR+G
6	*P. sublectaticum-clade*	7	460	HKY+I	524	GTR+G	888	GTR+G
7	*P. verhagenii-clade*	11	481	K2+G	513	GTR+G+I	928	GTR+G
9	*P. lividum-clade*	20	487	K2+G	509	K2+I	937	K2+G
10	*P. hoeksii-clade*	10–11	473	GTR+I	539	GTR+G	930	GTR+G+I

species of section *Aspergilloides* share phenotypic characters such as vesiculate, monoverticillate conidiophores, a moderate to fast growth rate on CYA and/or MEA, and a negative Ehrlich reaction. Furthermore, many species of section *Aspergilloides* produce crusts of conidia on MEA that either shift or fall off in mass, similar to the characteristic colonies of *P. crustosum* (sect. *Penicillium*). This feature is most pronounced on DG18. Each clade is treated in detail below. Clades containing multiple species are analysed separately using *BenA*, *CaM* and *RPB2* sequences, and this data is often supported by phenotypic characters.

Clade 1: *Penicillium spinulosum*-clade

Species belonging to the *P. spinulosum*-clade are phenotypically similar to those of the *P. glabrum*-clade. Both clades contain species that grow rapidly on CYA, YES and MEA. Furthermore, they predominantly produce monoverticillate conidiophores with an inflated apex, and have globose to subglobose conidia that are finely to distinctly roughened, or spirally banded. No consistent phenotypic characters were found to distinguish the two clades. Generally, species that belong to the *P. glabrum*-clade produce velvety colonies and have darker green conidia on MEA and often an orange-brown reverse on YES, while species of the *P. spinulosum*-clade are more floccose, produce conidia in shades of pure or dull green and the reverse on YES lacks orange shades. Furthermore, the species of the *P. glabrum*-clade produce acid on CREA, a feature often absent in species of the *P. spinulosum*-clade, which grow poorly on CREA.

Eighteen species were placed in synonymy with *P. spinulosum* by Pitt (1980). Phylogenetically, eleven of these taxa belong to the *P. spinulosum*-clade: *P. abeanum*, *P. baiiolum*, *P. brunneoviride*, *P. flavocinereum*, *P. mediocre*, *P. mucosum*, *P. roseomaculatum*, *P. trzebinskii*, *P. trzebinskii* var. *magnum*, *P. tannophagum* and *P. tannophilum*. Four of the remaining species belong to other clades of section *Aspergilloides*: *P. paczowskii*, *P. terlikowskii* and *P. spinuloramigenum* belong to the *P. glabrum*-clade and *P. ardesiacum* (CBS 497.73^{T}) is a member of the *P. fuscum*-clade. Two species are phylogenetically unrelated to section *Aspergilloides*: *P. viridorsum* (CBS 269.29^{T}) is close to *P. cyclopium* and *P. citreovirens* (CBS 320.59^{T}) is close to *P. corylophilum*. The type culture of *P. janthocitrinum* (CBS 268.29^{T}) is dead in the CBS collection and we did not include this strain in our study. We follow Pitt (1980) and treat this species as a synonym of *P. spinulosum*. Subsequent to Pitt's monograph, *P. subericola* was described as a new species closely related to *P. spinulosum* (Barreto *et al.* 2011).

The type strains of the species that belong to the *P. spinulosum*-clade, together with freshly isolated strains from various substrates and localities, were subjected to a phylogenetic study. Combined analysis of three genes (*BenA*, *CaM* and *RPB2*) revealed the presence of three well-supported lineages in the *P. spinulosum*-clade (Fig. 3). One lineage is centred on the type of *P. spinulosum* (97 % ML, 1.00 pp). Basal to this lineage is a set of strains that is described below as *P. sterculiniicola* (100 % BS, 1.00 pp). The third lineage comprises *P. palmense* and *P. grancanariae* and has a basal position relative to the *P. spinulosum* and *P. sterculiniicola* lineages (100 % ML, 1.00 pp).

The clade containing many other strains previously identified as *P. spinulosum*, including the ex-neotype of *P. spinulosum* (CBS 374.48^{NT}) is subdivided into five well-supported lineages (>95 % ML, 1.00 pp) in the combined analysis, which are labelled clades 1–5. The topologies of the single gene phylograms are congruent with the combined phylogram. However, they are generally poorly resolved and only three of the five lineages have support (>70 % and >0.95 pp) (Figs 2, 3). No ex-type strains of any described species occur in clade 1 and 2. The single and combined sequence analysis (Figs 2, 3) shows that the two lineages are related, but distinct. No diagnostic phenotypic differences were observed among strains in these clades. Based on this data, we decided to describe these strains as a single species, *P. subspinulosum*. The type strains of *P. roseomaculatum* (CBS 137962), *P. baiiolum* (CBS 137254) and *P. subericola* (CBS 125096) belong to clade 5. Barreto *et al.* (2011) described *P. subericola* but the types of *P. roseomaculatum* and *P. baiiolum* were not included in that study. The latter two species were described by Biourge (1923) and predate *P. subericola*. As both were described in the same publication, neither has priority. We chose *P. roseomaculatum*, because the type strain of this species is in better condition than that of *P. baiiolum* and better resembles the other freshly isolated strains of this species. Clade 4 contains *P. spinulosum* and the ex-types of *P. tannophilum* (CBS 271.35^{T}), *P. brunneoviride* (CBS 137257; probably type, Pitt (1980: 180)), *P. mucosum* (CBS

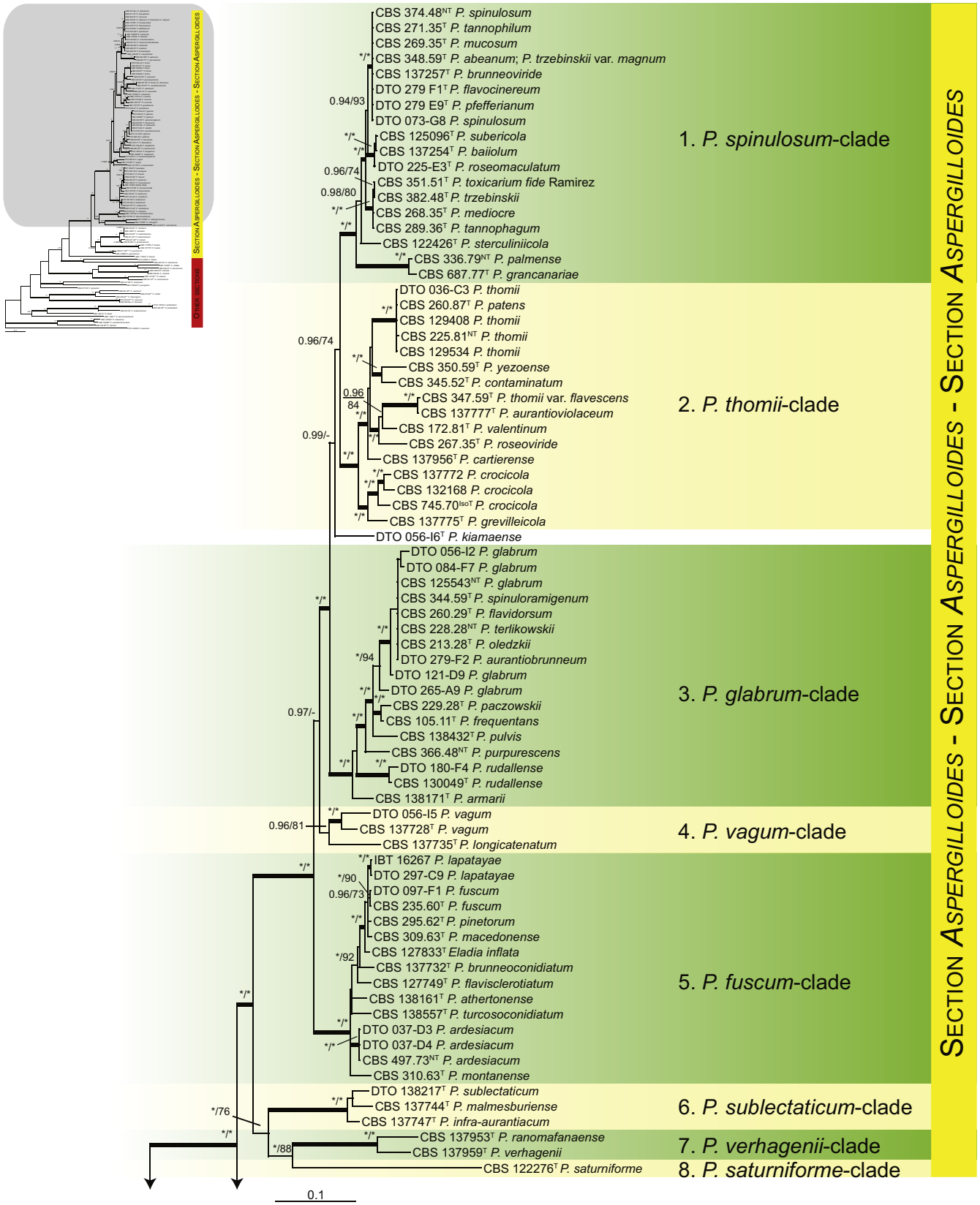

Fig. 1. Phylogenetic tree inferred from the concatenated nucleotide matrix (partial *BenA*, *CaM* and *RPB2* sequences) using Bayesian inference showing the relationship of species accommodated in section *Aspergilloides*. With exception of *P. thiersii*, all species of section *Aspergilloides* for a well-supported lineage. The bar indicates the number of substitutions per site. The phylogram is rooted with *Penicillium expansum* (ATCC 24692).

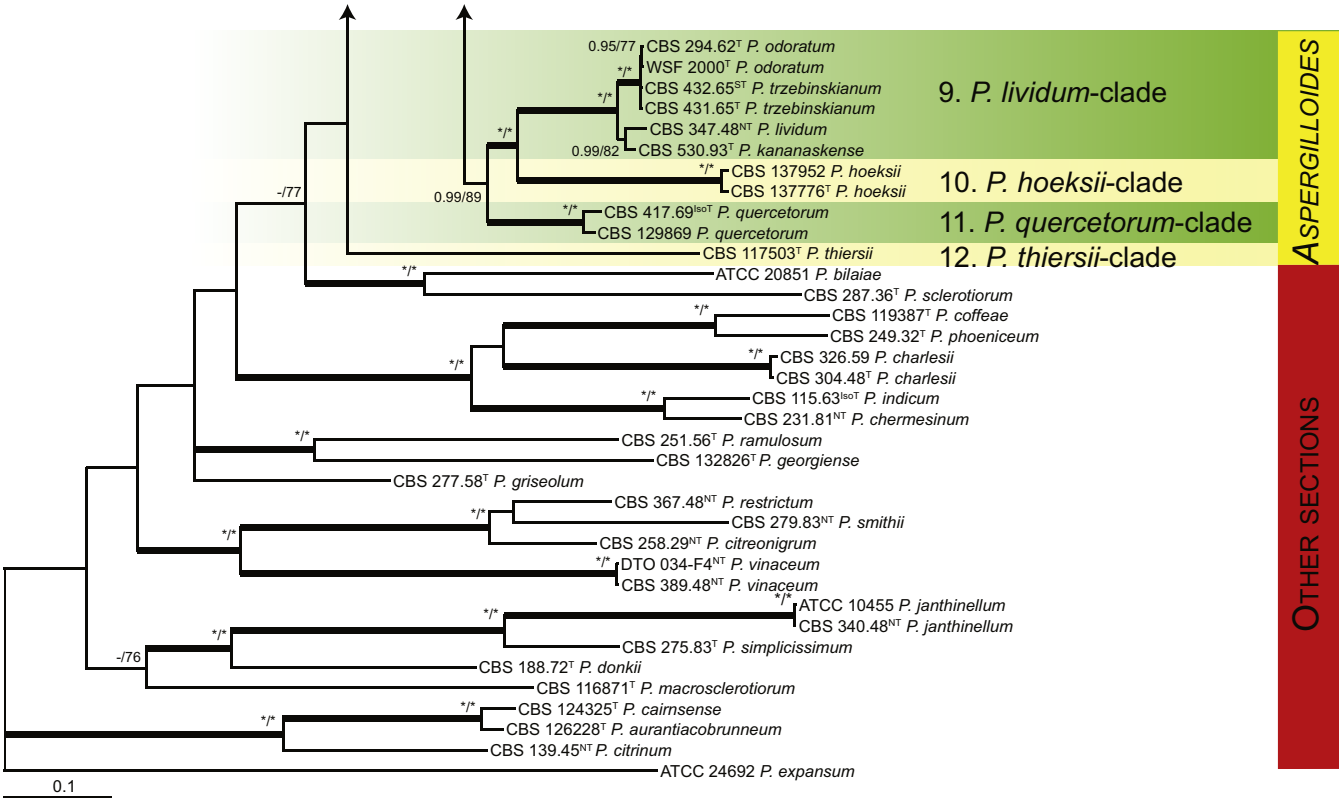

Fig. 1. (Continued).

269.35T), *P. flavocinereum* (CBS 137964 = NRRL 2051), *P. abeanum* and *P. trzebinskii* var. *magnum* (CBS 348.59). In addition, NRRL 727 (= CBS 137963), a strain identified as *P. pfefferianum* by Westling belongs to this clade, confirming the conclusions of Raper & Thom (1949: 184) and Pitt (1980: 177). Pitt (1980) discussed in detail the differences between *Citromyces pfefferianus* Wehmer and *P. pfefferianum* (Wehmer) Westling and we follow his conclusions by maintaining *C. pfefferianus* a synonym of *P. glabrum*. *Penicillium tannophagum* (CBS 289.36T), *P. mediocre* (CBS 268.35T), *P. trzebinskii* (CBS 382.48T) and *P. toxicarium fide* Ramírez (CBS 351.51T) belong to the same lineage (clade 3). *Penicillium toxicarium* Miyake was described without a Latin diagnosis but was validated by Ramírez (1982) based on CBS 351.51. However, Miyake's description of *P. toxicarium* does not correspond with that of Ramírez, making this validation problematic. *Penicillium trzebinskii* was described by Zaleski (1927) and predates *Penicillium tannophagum* and *P. mediocre*, which were both described in 1935.

Thus, seven species are accepted in the *P. spinulosum*-clade: *P. sterculiniicola*, *P. grancanariae*, *P. palmense*, *P. roseomaculatum*, *P. spinulosum*, *P. subspinulosum* and *P. trzebinskii*. A summary of their phenotypic characters is given in Table 3. *Penicillium spinulosum*, *P. roseomaculatum*, *P. trzebinskii* and *P. subspinulosum* are phylogenetically and phenotypically closely related. These species can be differentiated by growth characters on CYA, CREA and MEA. On CYA and MEA, *P. spinulosum* generally grows faster than the other species; however, there is an overlap in diameters (Table 3). *Penicillium spinulosum* and *P. subspinulosum* have similar cream or (pale) brown reverse colours on CYA. In comparison, reverse colours of *P. trzebinskii* are yellow or light orange-brown in the centre. The reverse of the investigated *P. roseomaculatum* strains vary and can be cream coloured as in *P. spinulosum* and *P. subspinulosum*, but can also be in shades of light brown or yellow. The colony texture on CYA and MEA differentiates *P. subspinulosum* from the other species. Colonies of *P. subspinulosum* have a velvety texture on CYA and are velvety with a floccose centre on MEA. The other species have floccose colonies on CYA and MEA. Growth on CREA distinguishes *P. subspinulosum* and *P. trzebinskii* from *P. spinulosum*. The latter grows well on CREA and produces acidic compounds followed by base (delayed reaction, 11 d), while *P. subspinulosum* and *P. trzebinskii* grew poorly on CREA and did not produce acidic compounds. Strains belonging to *P. roseomaculatum* had variable growth characters on CREA. Growth was either poor (*n* = 2) or good (*n* = 6). The strains with poor growth on CREA (DTO 035-A1, DTO 057-A2) also did not produce acidic compounds; the others were poor or moderate acid producers. The colony diameter on CYA incubated at 30 °C was informative because *P. spinulosum* and *P. trzebinskii* generally have larger colonies than *P. subspinulosum*. As with its growth on CREA, there was also a large variation among strains of *P. roseomaculatum* on CYA. Growth at 30 °C was slow (8–12 mm) in some strains, while others grew fast (22–29 mm).

Penicillium grancanariae and *P. palmense* were both isolated from air in Gran Canaria, Spain. These species produce ellipsoidal and finely roughened conidia, while the other *P. spinulosum*-clade species have globose or subglobose conidia which are (distinctly) spirally banded. *Penicillium grancanariae* was placed in synonymy with *P. thomii*, and *P. palmense* was accepted in the list of accepted *Penicillium* species (Frisvad *et al.* 1990, Pitt *et al.* 2000). Based on *CaM* and *BenA* sequences, these species were considered conspecific in the study of Barreto *et al.* (2011). We treat these species as distinct based on our combined *BenA*, *CaM* and *RPB2* sequence analysis in combination with phenotypic characteristics (Table 3). *Penicillium*

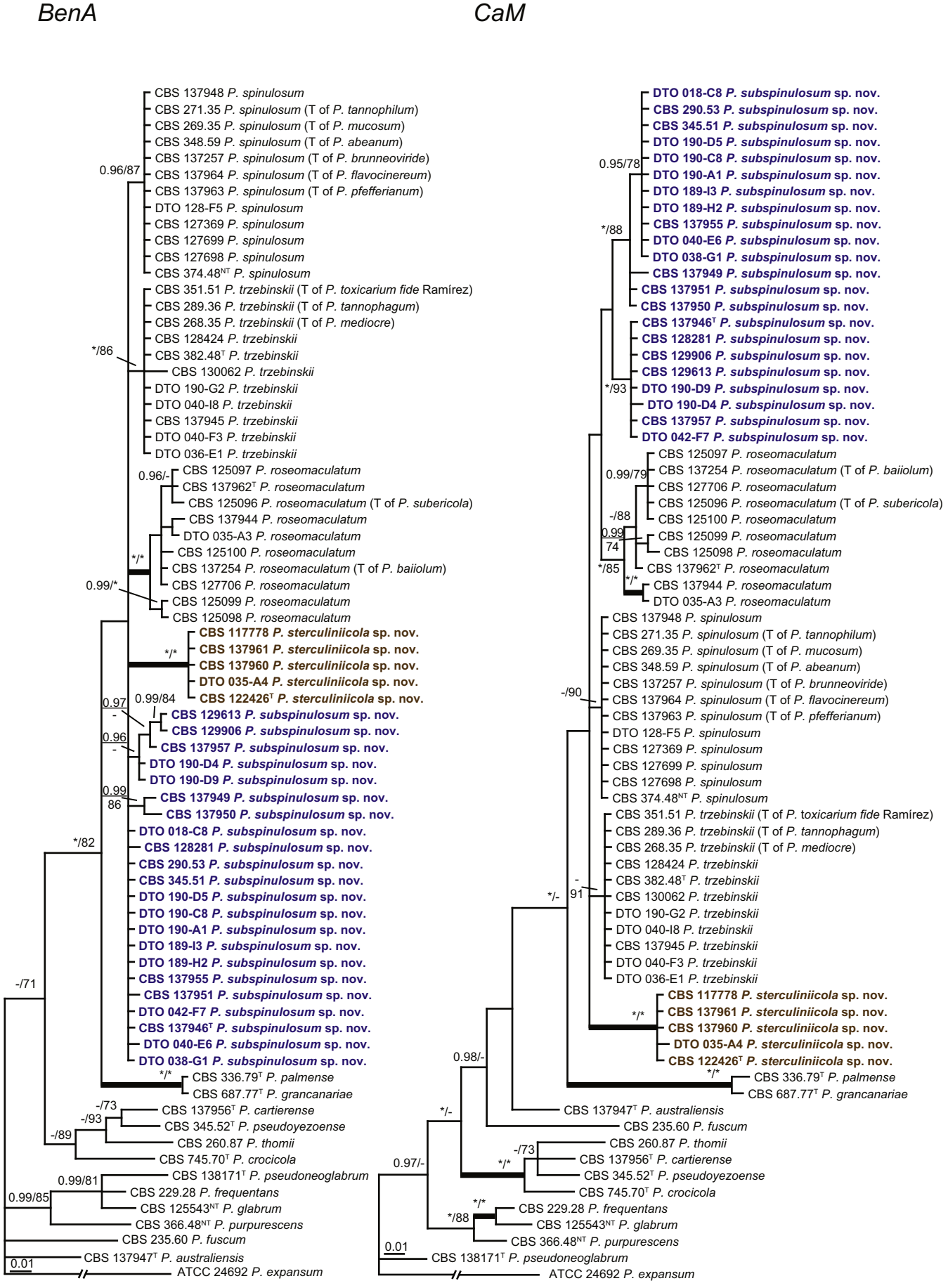

Fig. 2. Phylogenetic trees showing the relationship among strains belonging to the *P. spinulosum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

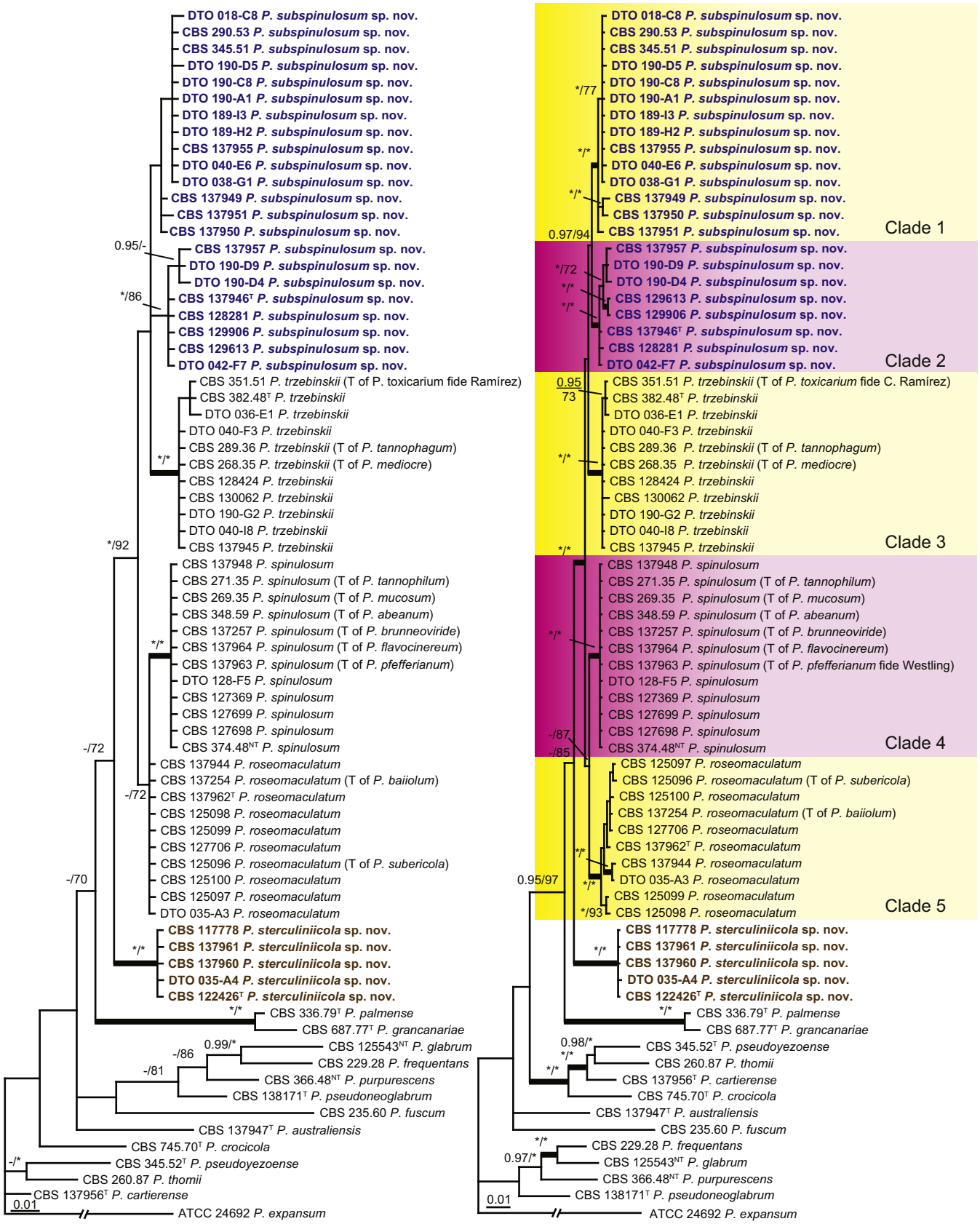

Fig. 3. Phylogenetic trees showing the relationship among strains belonging to the *P. spinulosum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

Table 3. Overview of diagnostic characters of species belonging to the *P. spinulosum*-clade.

Species name	Colony diam on CYA (mm)	Sporulation on CYA	Colony diam on MEA (mm)	Colony texture on MEA	Growth on CREA	Acid / base production on CREA	CYA30°C	Conidial ornamentation
P. grancanariae	34–38	Poor	42–46	Floccose	Poor	Poor	16–21	Finely rough
P. palmense	31–34	Good	35–41	Velvety	Poor	Absent	24–26	Finely rough
P. spinulosum	(34–)39–52	Variable: poor to good	(41–)46–52	Floccose	Good	Poor to moderate	20–30	Rough
P. sterculiniicola	(27–)40–45	Absent	(39–)43–53	Variable: velvety to floccose	Good	Moderate	(29–)39–44	Distinctly rough
P. trzebinskii	(25–)37–41	Variable: absent to moderate	(26–)30–39(–42)	Floccose	Variable: poor or good	Variable: absent to moderate	Two groups: 8–12 or 22–29	Finely rough
P. subspinulosum	(24–)36–41	Variable: absent to moderate	(28–)35–42	Floccose at centre, velvet at edge	Poor	Absent	4–18(–22)	Finely to distinctly rough
P. tannophagum	(25–)42–51	Variable: poor to moderate	35–45	Floccose	Poor	Absent	(10–)17–26(–34)	Finely rough

sterculiniicola is phylogenetically and phenotypically distinct. It differs from other *P. spinulosum*-clade species by its high growth rate on CYA when incubated at 30 °C ((29–)37–47 mm) and 33 °C (15–24 mm) (Table 3, Fig. 4).

Clade 2: *Penicillium thomii*-clade

Species that belong to the *P. thomii-clade* are phylogenetically related to species of the *P. spinulosum*-clade (Fig. 1; 74 % ML, 0.96 pp), and basal to these two lineages is the *P. glabrum*-clade. Species belonging to the *P. thomii*-clade share characters with species of the *P. glabrum*- and *P. spinulosum*-clades such as a fast growth on CYA, MEA and YES, growth on CYA incubated at 30 °C ((5–)15–35(–45) mm) and conidiophores that are predominantly monoverticillate with a vesiculate apex. There are also phenotypic differences among these clades. Species of the *P. thomii*-clade differ from most other species of section *Aspergilloides* by the production of hard, gritty sclerotia, which are often in shades of pink on OA (orange-pink, brownish pink). The conidiophores are 200–400 µm long, with roughened walls and conidia are (broadly) ellipsoidal or fusiform. Our description of the *P. thomii*-clade corresponds with Pitt's description of the morphospecies *P. thomii* (Pitt 1980).

Based on the presented phylogenies, 12 species are accepted in the *P. thomii*-clade (Figs 5, 6). Seven species were previously described (*P. aurantioviolaceum*, *P. crocicola*, *P. fusisporum*, *P. roseoviride*, *P. thomii*, *P. valentinum*, *P. yezoense*), one is in the process of being described elsewhere (*P. jejuense*, M.S. Park *et al.* submitted) and four are described here as new (*P. austroafricanum*, *P. cartierense*, *P. contaminatum*, *P. grevilleicola*). Pitt (1980) synonymised six species and one variety with *P. thomii*. *Penicillium aurantioviolaceum*, *P. crocicola*, *P. roseoviride*, *P. valentinum* and *P. yezoense* were treated as synonyms of *P. thomii* by Pitt (1980) and are accepted as distinct species in this study. *Penicillium yezoense* was described without a Latin description and is validated in the taxonomy section below. *Penicillium parallelosporum* and *P. thomii* var. *flavescens* were also regarded as synonyms of *P. thomii* (Pitt 1980). The type culture of *P. parallelosporum* (CBS 159.69) is dead in the CBS collection and could not be included in our study. However, this name does not compete with the other names because it was invalidly described, lacking a Latin diagnosis. *Penicillium thomii* var. *flavescens* was also described without a Latin diagnosis and the type strain of this species (CBS 347.59^{T}) is placed in synonymy with *P. aurantioviolaceum*. The accepted species *P. valentinum* was described in 1980, after the publication of Pitt's monograph. The species was synonymised with *P. thomii* (Frisvad *et al.* 1990), but has distinct *BenA*, *CaM* and *RPB2* sequences. Our phylogenies show that *P. patens* (CBS 260.87^{T}) is a synonym of *P. thomii*. It was placed near *P. donkii* based on its non-vesiculate conidiophores and soft, pale brown sclerotia (Pitt & Hocking 1985), but Frisvad *et al.* (1990) already noted a close relation of this species with *P. thomii*.

The result of the combined analysis of *BenA*, *CaM* and *RPB2* sequences of isolates belonging to the *P. thomii*-clade is shown in Fig. 6. The deeper nodes of this phylogeny are poorly resolved. *Penicillium crocicola*, *P. austroafricanum*, *P. jejuense* and *P. grevilleicola* form well-supported lineages on a well-supported branch (0.97 pp, >95 % ML). The other species are resolved in one clade in Fig. 1; however, this is not

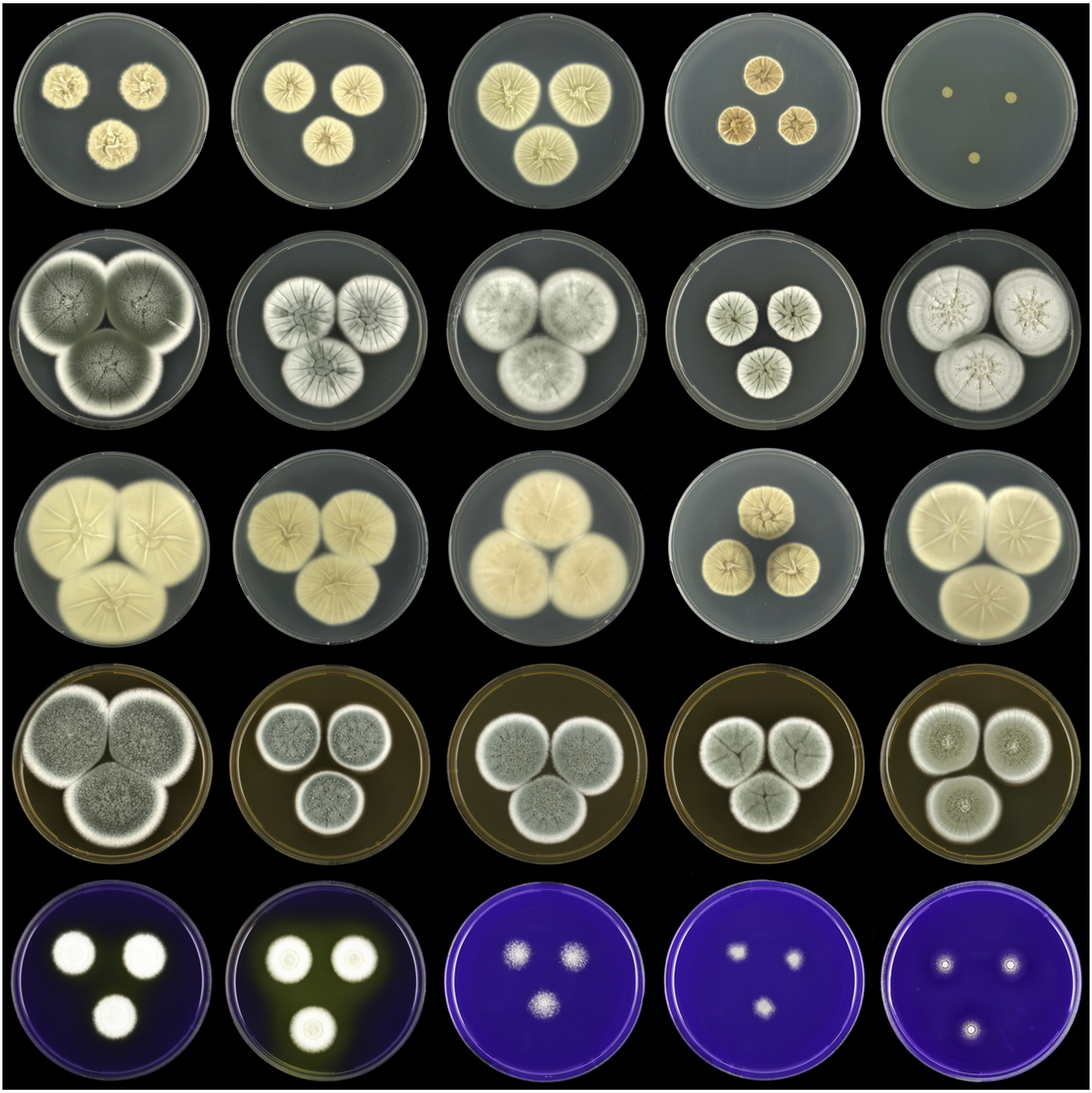

Fig. 4. Overview of growth characters of *P. spinulosum* and related species. Columns, left to right: *P. spinulosum*, *P. roseomaculatum* DTO 084-F8, *P. roseomaculatum* DTO 057-A2, *P. trzebinskii*, *P. subspinulosum*. Rows, top to bottom: CYA30°C reverse, CYA obverse, CYA reverse, MEA obverse, CREA obverse.

observed in the combined analysis of the *P. thomii*-clade (Fig. 6). *Penicillium yezoense* and *P. contaminatum* are sister species in Fig. 1, as are *P. aurantioviolaceum*, *P. roseoviride* and *P. valentinum*. No statistical support for this observation is found in Fig. 6. The phylogenies based on the individual data sets are congruent. Sequence variation is present within *P. crocicola* and *P. jejuense*. The *P. crocicola* lineage has no support in the *BenA* and *CaM* phylograms and weak support in the *RPB2* analysis (82 % ML, 77 % MP). In the individual phylogenies, CBS 132168, CBS 137754 and CBS 745.70 (ex-type strain of *P. crocicola*) sit outside the main *P. crocicola* clade. These single strains have slightly different phenotypes than the strains belonging to the main clade. For example, CBS 745.70 grows quickly on CYA30°C (40–45 mm) and does not produce acidic compounds on CREA, and CBS 132168 differs by the formation of light yellow mycelium on YES and a slower lower growth rate on CYA30°C (15–20 mm *vs* 25–35 mm by the main group of *P. crocicola* isolates). These isolates might represent new species, but their description is deferred until more strains are collected and examined. Similarly, sequence variation is observed in *P. jejuense*. In the *CaM* and *RPB2* data sets, CBS 137774 and CBS 137755 cluster together on a well-supported branch, separate from the type of the species. This grouping is not observed in the *BenA* data set; however, the bootstrap value was low in the MP analysis. The type strain of *P. jejuense* was unavailable for examination and no phenotypic comparison among the *P. jejuense* isolates was undertaken. The new species *P. austroafricanum*, *P. cartierense*, *P. contaminatum* and *P. grevilleicola* are described in the taxonomy part of this paper and phenotypic characters to differentiate between those species and their closest relatives are provided there.

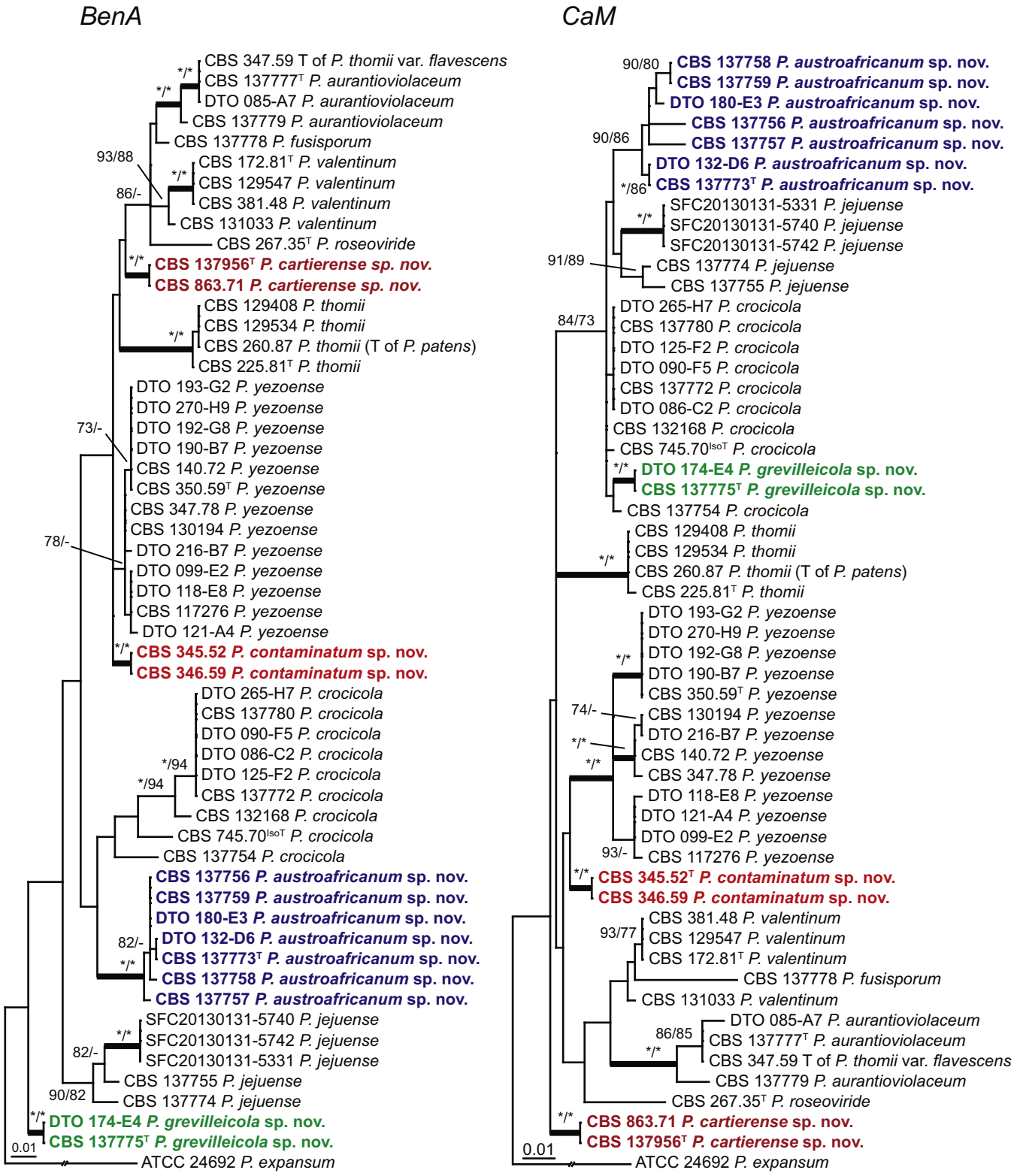

Fig. 5. Phylogenetic trees showing the relationship among strains belonging to the *P. thomii*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

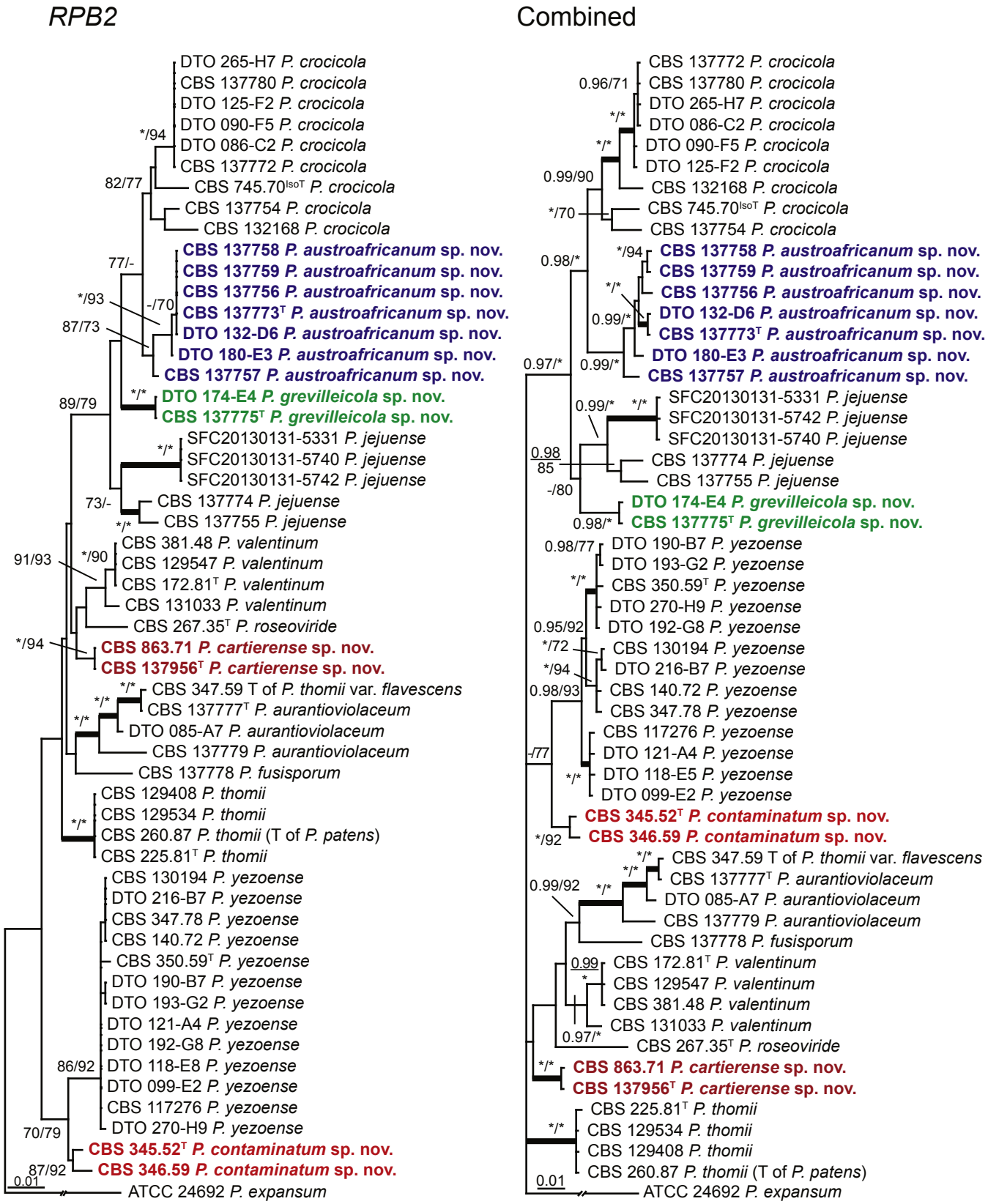

Fig. 6. Phylogenetic trees showing the relationship among strains belonging to the *P. thomii*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

Clade 3: *Penicillium glabrum*-clade

As mentioned above, species belonging to the *P. glabrum*-clade are phenotypically closely related to those of the *P. spinulosum*-clade. A high degree of sequence variation was observed in the *BenA*, *CaM* and *RPB2* data sets. Based on the phylogenies, combined with phenotypic observations, this study focus on seven lineages (Figs 7, 8). Six of the seven lineages are well-supported in the combined analysis and the lineage containing isolate CBS 138160 is only supported in the ML analysis (82 % ML). The two main lineages in our analysis of the *P. glabrum*-clade are centred on the ex-types of *P. glabrum* (CBS 125543^{NT}) and *P. frequentans* (CBS 105.11^{T}). Another lineage includes the type of *P. purpurescens* (CBS 366.48^{T}). The remaining lineages are described here as new species, namely *P. armarii*, *P. bussumense*, *P. pulvis* and *P. rudallense*. Analysis of the individual *BenA*, *CaM* and *RPB2* partitions resulted in poorly resolved phylograms with many polytomies and generally lacking branch support (Figs 7, 8). In the *BenA* and *CaM* phylograms, the *P. frequentans* and *P. glabrum* strains do not resolve in two lineages. On the other hand, because of the lack of support of the nodes, this does not result in incongruency between the phylograms, hence the recognition of the two distinct species. In contrast, both species are resolved in the *RPB2* phylogram with moderate to good support (80 % ML, 1.00 pp for *P. glabrum*; 70 % ML, 1.00 pp for *P. frequentans*). A large sequence variation is present in the currently proposed delineation of *P. glabrum*. A variation of 4.0 % was observed among the *BenA* sequences. Less variation is detected in the *CaM* data set (2.0 %) and the least variation was present in the *RPB2* data set (1.4 %). This high degree of sequence variation is not reported in other *Penicillium* sections. In contrast, some species (e.g. *P. commune*, *P. camemberti* and *P. caseifulvum*) share *BenA* sequences or can only be differentiated by one base pair difference (Samson *et al.* 2004, Houbraken *et al.* 2011a, b). The phylogenetic placement of *P. bussumense* (CBS 138160^{T}) also needs further attention. Strain CBS 138160^{T} takes a distinct position in the *BenA* phylogram, and it is among the *P. frequentans* strains in the *CaM* analysis. Similarly as in *P. glabrum*/*P. frequentans*, both phylograms lack statistical support and this strain is resolved in the *RPB2* data set.

Two species belonging to the *P. glabrum*-clade, *P. glabrum* and *P. purpurescens*, were accepted in previous studies (Pitt 1980, Pitt *et al.* 2000, Barreto *et al.* 2011). *Citromyces purpurescens*, *Citromyces virido-albus*, *Penicillium virido-album*, *P. internascens* and *P. resinae* are synonyms of *P. purpurescens* (see Taxonomy). Houbraken & Samson (2011) incorrectly used CBS 324.83 as a representative of *P. asperosporum*; this strain is actually the ex-type of *P. resinae*. Comparison of the *RPB2* sequence of this strain deposited in GenBank (JN406574) with sequences generated in this study shows that CBS 324.83 is actually *P. purpurescens*. Several species were previously placed in synonymy with *P. glabrum* and one, *P. frequentans*, is re-introduced here. Based on our sequence data, *P. paczowskii* (CBS 229.28^{T}) is a synonym of *P. frequentans* (Figs 7, 8). The name *P. frequentans* was used by Raper & Thom (1949), but this name is predated by *P. glabrum* (Subramanian 1971, Pitt 1980). Interestingly, Raper & Thom's concept of *P. frequentans* was not based on the type strain of *P. frequentans*, but on NRRL 1915 (= CBS 328.48). This strain is currently identified as *P. glabrum* and this indicates that Raper & Thom's description of *P. frequentans* and Pitt's concept of *P. glabrum* are based on a similar set of isolates that differs from our concept. Recently, a strain identified as *P. glabrum* (DAOM 239074) had its genome sequenced and this isolate is re-identified here as *P. frequentans*.

Penicillium aurantiobrunneum (CBS 138433^{NT}), *P. flavidorsum* (CBS 260.29^{T}), *P. oledskii* (CBS 213.28^{T}) remain synonyms of *P. glabrum*. *Penicillium terlikowskii* (CBS 228.28^{T}) and *P. spinuloramigenum* (CBS 344.59^{T}), previously listed as synonyms of *P. spinulosum*, are treated here as synonyms of *P. glabrum*. Remarkably, combined sequence analysis (Fig. 8) shows that all the ex-type strains of *P. glabrum* and related synonyms belong to the same lineage, indicating a high genetic similarity. The reason for this bias remains unknown, but could be due to the fact that this sequence-type predominates in nature. *Penicillium candidofulvum* was listed by Pitt (1980) as a synonym of *P. glabrum* and a BLAST search with the ITS sequence of the ex-type strain for this species (CBS 254.37^{T}) has 100 % homology with the type strain of *P. corylophilum* (FRR 802^{NT}; AY373906). No type culture is available of *P. fluitans*. We follow Raper & Thom (1949) and Pitt (1980) and treat this species as a synonym of *P. glabrum*. *Penicillium trzebinskii* was treated as a synonym of *P. glabrum* by Barreto *et al.* (2011), but this was based on an incorrectly identified strain (CBS 328.48). Our results shows that the type of *P. trzebinskii* (CBS 382.48^{T}) is a distinct species belonging to the *P. spinulosum*-clade.

In this study we accept seven species in the *P. glabrum*-clade: *P. glabrum*, *P. purpurescens*, *P. frequentans*, *P. armarii*, *P. pulvis*, *P. rudallense* and *P. bussumense*. These species are phenotypically similar and an overview of characters to differentiate them is given in Fig. 9 and Table 4. *Penicillium purpurescens* and *P. armarii* differ from the other species by their conidial size (3.2–4.0 µm *vs* 2.5–3.2(–3.5) µm in other *P. glabrum*-clade species) and they differ from each other by their colony diameters on CYA and CYA30°C, and the degree of growth on CREA. *Penicillium glabrum* and *P. frequentans* are phylogenetically and phenotypically closely related. *Penicillium frequentans* strains have a (yellow) brown reverse on CYA incubated at 27 °C and 30 °C, while those of *P. glabrum* are in shades of beige-brown resulting in less warm colours. Furthermore, strains of *P. glabrum* tend to have a higher growth rate on CYA30°C, but there is an overlap in colony diameters. These observations are supported by extrolite data. The extrolite profiles of these two species differ and *P. frequentans* strains produce 6-methylisocoumarin and a compound with the same chromophore as pyranonigrin, while *P. glabrum* isolates are characterised by the production of citromycetin, fulvic acid, asterric acid, bisdechlorgeodin, geodin, sulochrin, and similar polyketides (Hetherington & Raistrick 1931, Mahmoodian & Stickings 1964). *Penicillium bussumense* can be differentiated from other related species by a CYAS:CYA ratio of 0.95–1.05 and smaller colonies on CYA. *Penicillium pulvis* has a (dark) brown reverse on CYA and YES, and brown soluble pigments on CYA; a feature not observed in any of the closely related species. *Penicillium rudallense* has distinctly ornamented dark green conidia which measure 3.0–3.5 µm diam.

Clade 4: *Penicillium vagum*-clade

The *P. vagum*-clade forms a well-supported lineage (>95 % ML; 1.00 pp) together with the *P. glabrum*, *P. thomii*, *P. spinulosum*

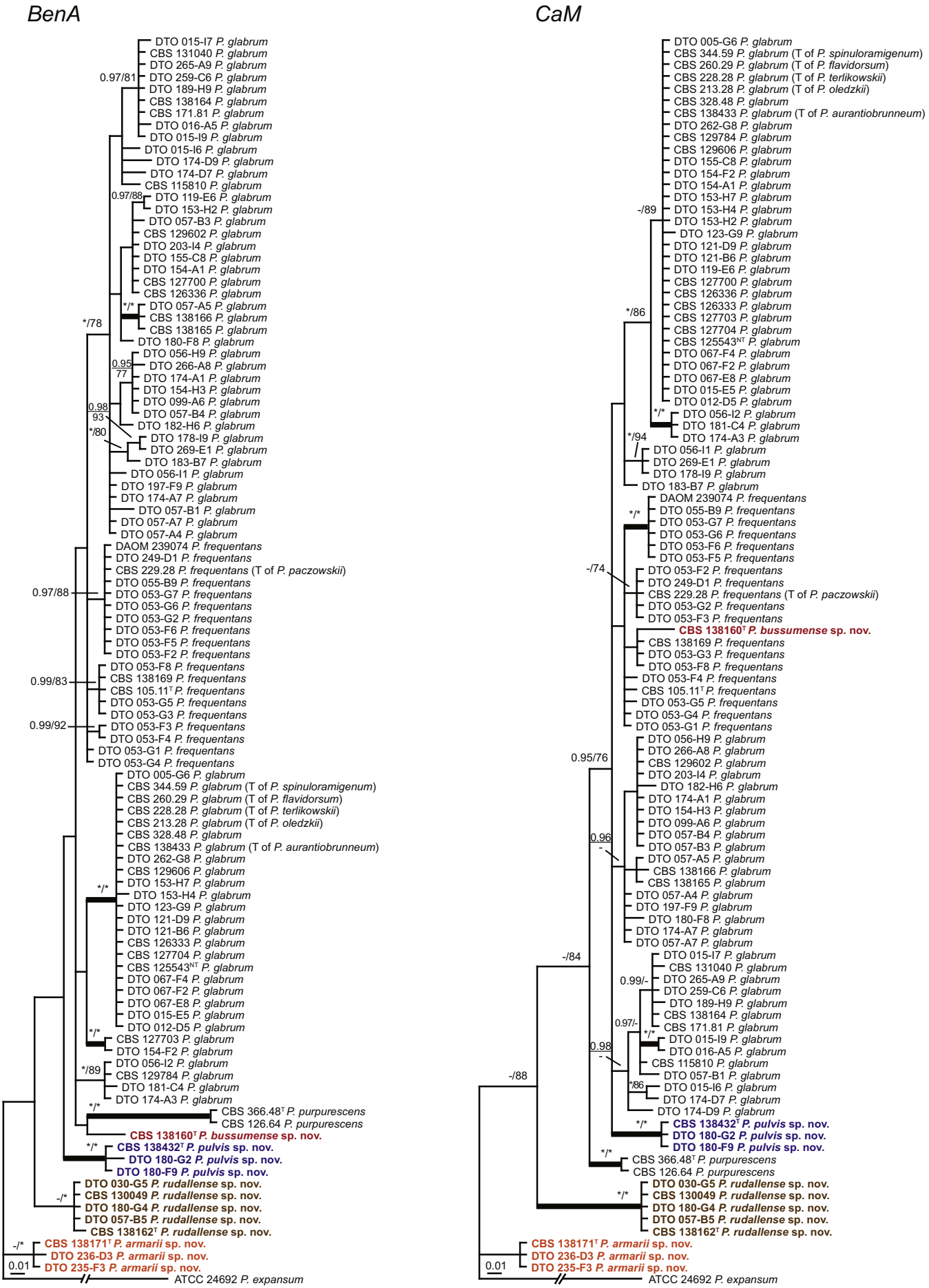

Fig. 7. Phylogenetic trees showing the relationship among strains belonging to the *P. glabrum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

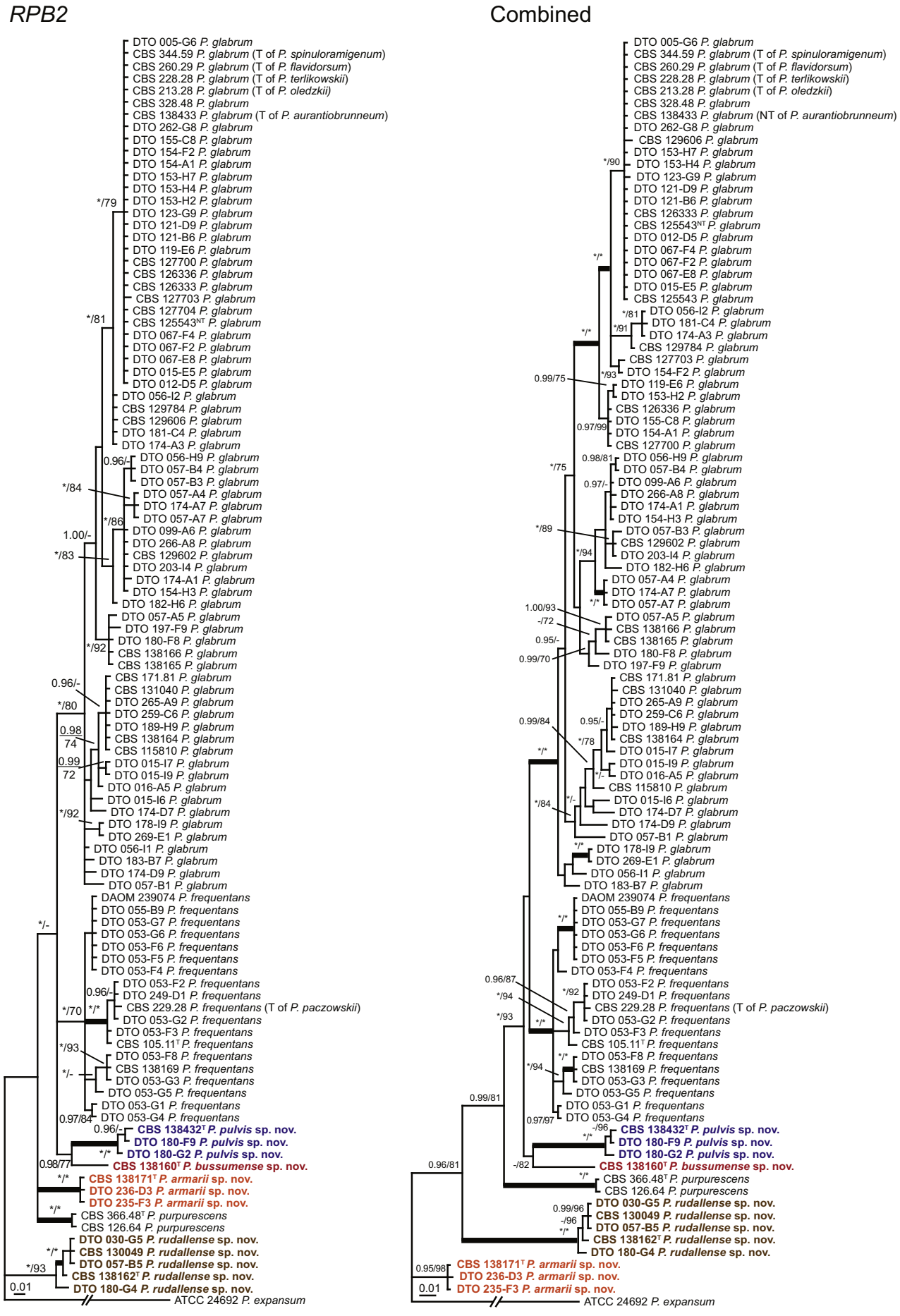

Fig. 8. Phylogenetic trees showing the relationship among isolates belonging to the *P. glabrum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

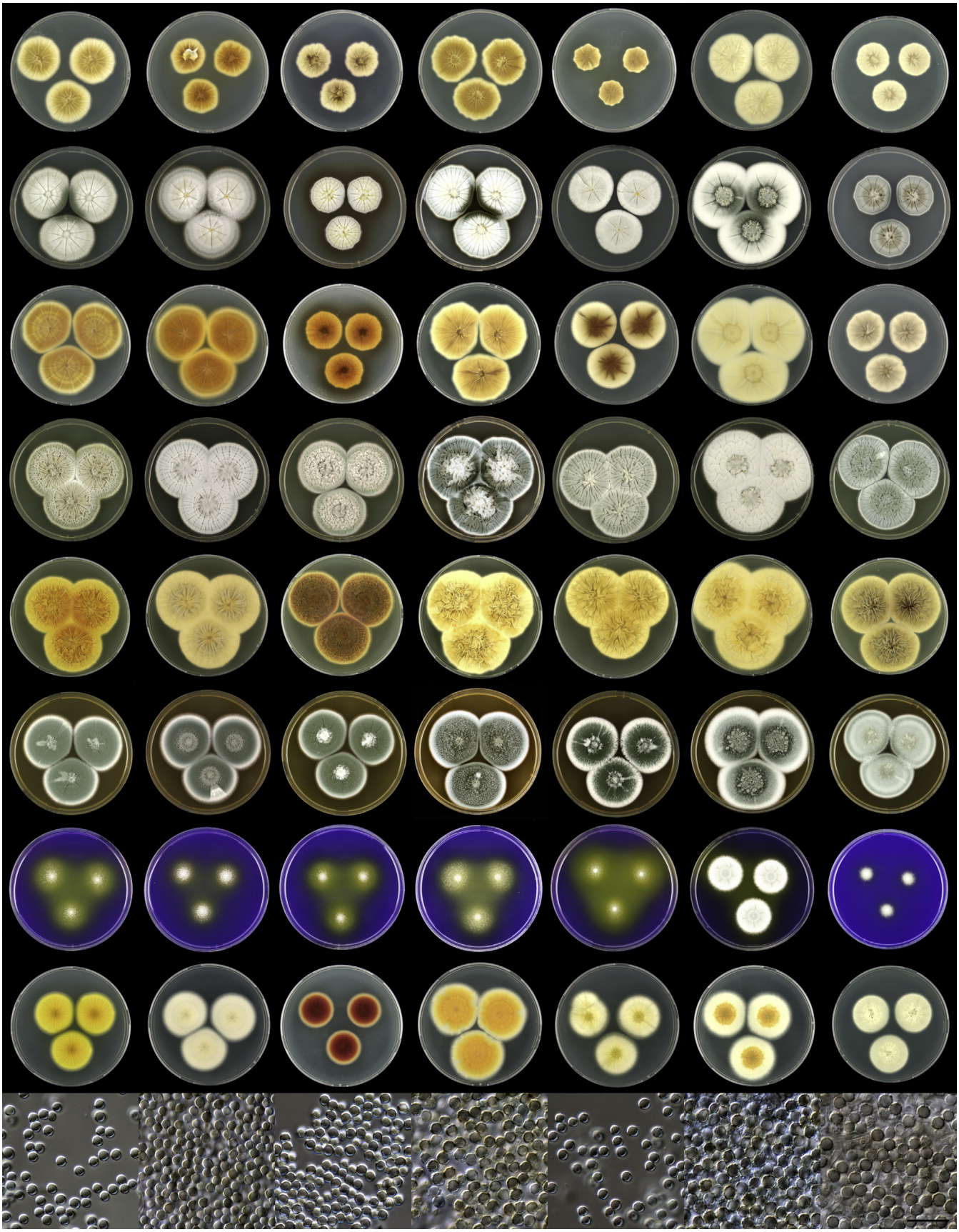

Fig. 9. Overview of growth characters of *P. glabrum*-clade species. Columns, left to right: *P. glabrum*, *P. frequentans*, *P. pulvis*, *P. rudallense*, *P. bussumense*, *P. armarii*, *P. purpurescens*. Rows, top to bottom: CYA30°C reverse, CYA obverse, CYA reverse, YES obverse, YES reverse, MEA obverse, CREA obverse, DG18 reverse, conidia. Scale bar = 10 µm.

Table 4. Overview of diagnostic characters of species belonging to the *P. glabrum*-clade.

Species name	CYA	MEA	YES	CYA30°C	CYAS:CYA	Growth on CREA	Conidial size (µm)	Conidial ornamentation
P. armarii	50–56	54–60	51–57	46–52	0.60–0.70	Good	3.2–4.0	Rough
P. bussumense	31–37	38–44	40–45	15–20	0.95–1.05	Weak	2.7–3.2	Finely rough
P. frequentans	(33–)38–50	38–51	40–53	21–32	0.80–0.95	Weak (occasionally good)	2.5–3.0	Finely rough to rough
P. glabrum	(30–)35–48	(30–)38–50	40–59	25–43	0.75–0.85	Weak	2.5–3.0	Finely rough
P. pulvis	26–32	37–43	39–45	24–30	0.75–0.90	Weak	2.7–3.2	Finely rough
P. purpurescens	31–37	40–50	42–50	22–28	0.92–0.97	Weak	3.2–4.0	Rough
P. rudallense	35–46	39–46	48–54	25–37	0.80–0.92	Weak	3.0–3.5	Rough

and *P. fuscum*-clade. The relation between the isolates belonging to the *P. vagum*-clade is moderately supported (Fig. 1; 81 % ML; 0.96 pp). The isolates that belong to this clade can be divided in two lineages (Figs 10, 11). These two lineages are phenotypically unrelated and share characters such as monoverticillate conidiophores and the production of globose and subglobose conidia; characters that are also observed in many other section *Aspergilloides* species. The moderate support in the phylogenetic analysis, combined with the phenotypic differences, indicate that these species are only loosely related. Based on the unique phylogenetic placement of these isolates, combined with phenotypic differences, these two lineages are described as new species: *P. vagum* and *P. longicatenatum*.

Based on the single gene phylogenies, the isolates that belong to the *P. vagum*-clade can be divided into two supported lineages (Figs 10, 11). The only strongly supported branch contradictory to this arrangement is the position of DTO 056-I5 in the *CaM* analysis. This isolate is basal to the *P. vagum* and *P. longicatenatum* clades in the *CaM* analysis, but belongs to the *P. vagum*-clade in the *BenA* and *RPB2* analysis. *Penicillium vagum* produces thick walled, spiny conidia and has a moderate acid production on CREA. In contrast, conidia of *P. longicatenatum* are finely roughened and isolates do not produce acidic compounds on CREA. A typical feature of *P. longicatenatum* is the abundant production of sclerotia on CYA and MEA. A detailed description of both species is given in the taxonomy section below.

Clade 5: *Penicillium fuscum*-clade

The *P. fuscum*-clade is phylogenetically related to the *P. spinulosum*-, *P. thomii*-, *P. glabrum*- and *P. vagum*-clades (>1.00 pp, >95 % ML) (Fig. 1). Species of the *P. fuscum*-clade differ from other species of sect. *Aspergilloides* by a slow or moderate growth rate on CYA [(10–)15–25(–30) mm] and CYAS (<15 mm), short stipes [10–80(–150) µm] and distinctly roughened, thick walled, globose to subglobose conidia.

The analysis of the separate *BenA* and *CaM* data sets resulted in poorly supported phylograms, while better support was obtained in the *RPB2* phylogram (Figs 12, 13). The phylograms are not congruent. In the *RPB2* phylogram, the isolates CBS 127833 (ex-type of *Eladia inflata*), CBS 130199 and CBS 129806 (indicated with ♣ symbol) group together with two other species on a branch with statistical support (86 % ML; 82 % MP) closer to *P. brunneoconidiatum* and *P. flavisclerotiatum*. In the *BenA* and *CaM* phylogenies, these isolates cluster with *P. fuscum* (*BenA*: 84 % ML, 82 % MP; *CaM*: 74 % ML, 82 % MP). The reason for this inconsistency is unknown, but it might indicate undersampling. The previously mentioned isolates are basal to *P. fuscum* in the combined analysis of the *BenA*, *CaM* and *RPB2* data sets (0.99 pp; >95 % ML) and we therefore tentatively identified all of these strains as *P. fuscum*.

Stolk (1968) found ascospores in an old culture of the type strain of *P. pinetorum* (CBS 295.62^{T}) and described this strain as *Eupenicillium pinetorum*. *Penicillium fuscum* was linked to *E. pinetorum* based on original descriptions and illustrations of *Citromyces fuscus* (Stolk & Samson 1983). This name predates *P. pinetorum* and was therefore accepted by Houbraken & Samson (2011). The species *P. silvaticum*, *P. macedonense* (Pitt 1980), *P. asperosporum* (≡ *P. echinosporum* G. Sm., non Nehira) and *P. montanense* were treated as synonyms of *P. fuscum* (Stolk & Samson 1983). *Penicillium macedonense* (CBS 309.63^{T}) and *P. silvaticum* (CBS 235.60^{T}) reside with *P. fuscum* (CBS 295.62^{NT}) in all phylogenies (Figs 12, 13) confirming their synonymy with *P. fuscum*. *Penicillium montanense* was placed in synonymy with *P. fuscum* by Stolk & Samson (1983), while other studies accepted this species as distinct (Pitt 1980, Pitt *et al.* 2000). The type strain of *P. montanense* (CBS 310.63^{T}) is distinct in our phylogenies of the *P. fuscum*-clade. *Penicillium asperosporum* was synonymised with *P. fuscum* by Stolk & Samson (1983), but was considered distinct in other studies (NRLL 3411^{T} = IMI 080450; Peterson 2000). Sequence analysis shows that this species is a synonym of *P. montanense* (see Taxonomy). The phylogenetic position of ex-type strain of *Eladia inflata* (CBS 127833^{T}) is uncertain (see above). We tentatively treat this species as a synonym of *P. fuscum*.

Based on our multigene phylogenies, nine species are accepted in the *P. fuscum*-clade. Three species were previously described (*P. fuscum*, *P. montanense* and *P. ardesiacum*) and six are newly introduced here: *P. athertonense*, *P. brunneoconidiatum*, *P. clavistipitatum*, *P. flavisclerotiatum*, *P. tsitsikammaense* and *P. turcosoconidiatum*. Conidiophore morphology is diagnostic for distinguishing these species. For example, *P. clavistipitatum* produces rough-walled stipes and *P. brunneoconidiatum* and *P. turcosoconidiatum* produce very short stipes. *Penicillium fuscum* is the only species in the clade producing ascospores and sclerotia are observed in *P. flavisclerotiatum* and *P. tsitsikammaense*. These species can be differentiated by the growth rate on CYA incubated at 25 and 30 °C. An overview of growth characters is given in Table 5.

Clade 6: *Penicillium sublectaticum*-clade

A set of six strains formed a discrete clade within section *Aspergilloides*, here named the *P. sublectaticum*-clade. These species are phylogenetically related to the *P. verhagenii* and

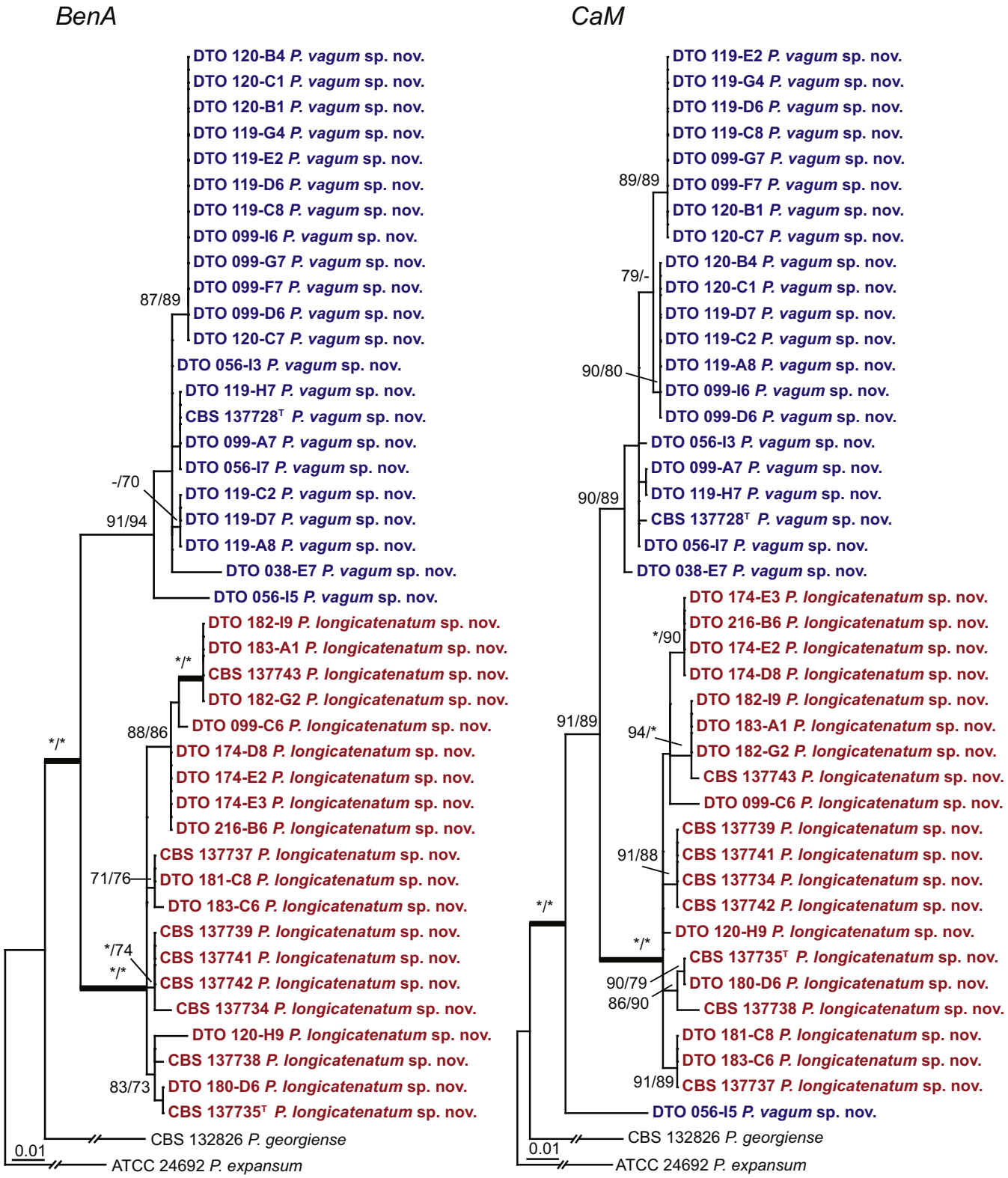

Fig. 10. Phylogenetic trees showing the relationship among strains belonging to the *P. vagum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

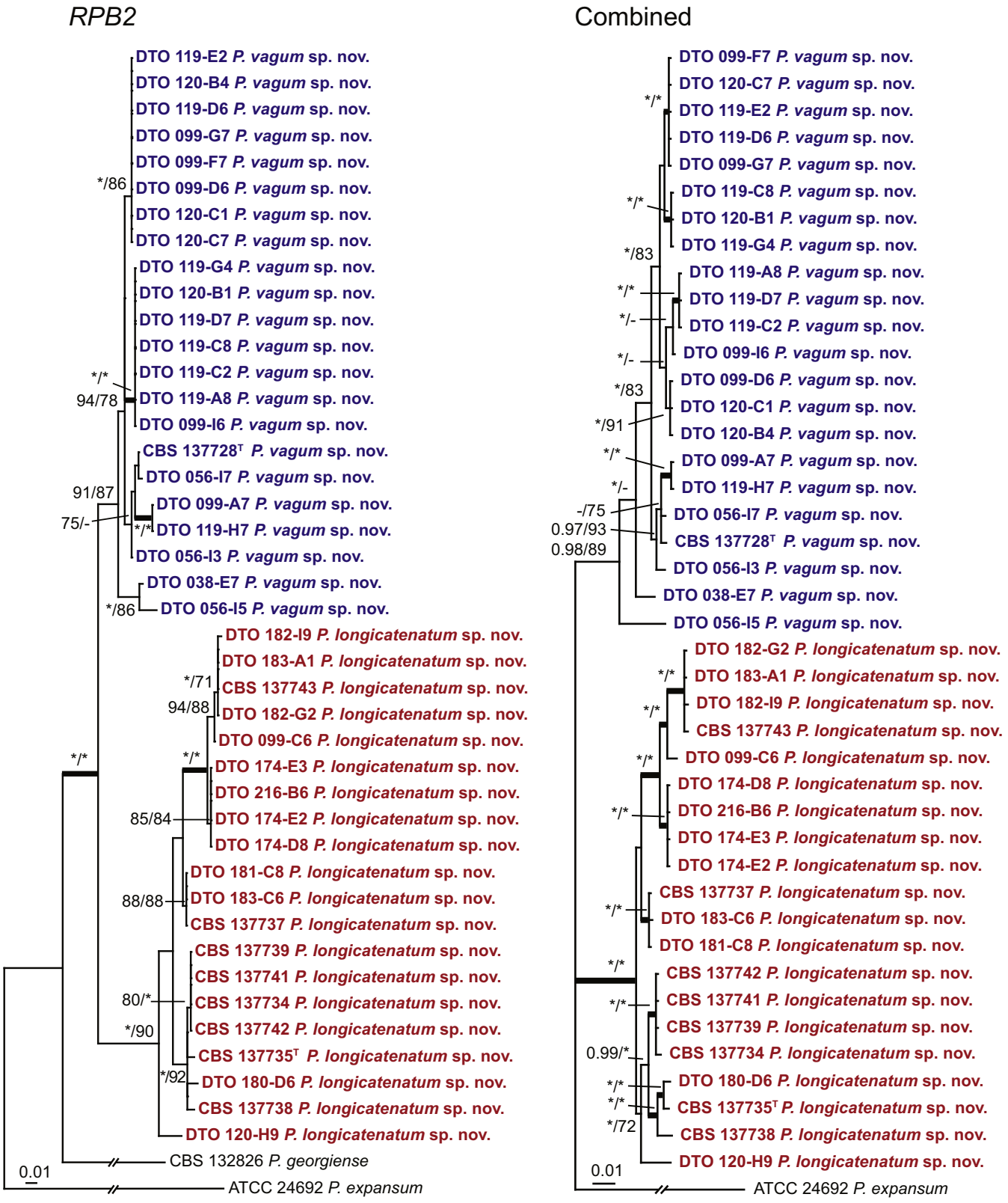

Fig. 11. Phylogenetic trees showing the relationship among strains belonging to the *P. vagum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

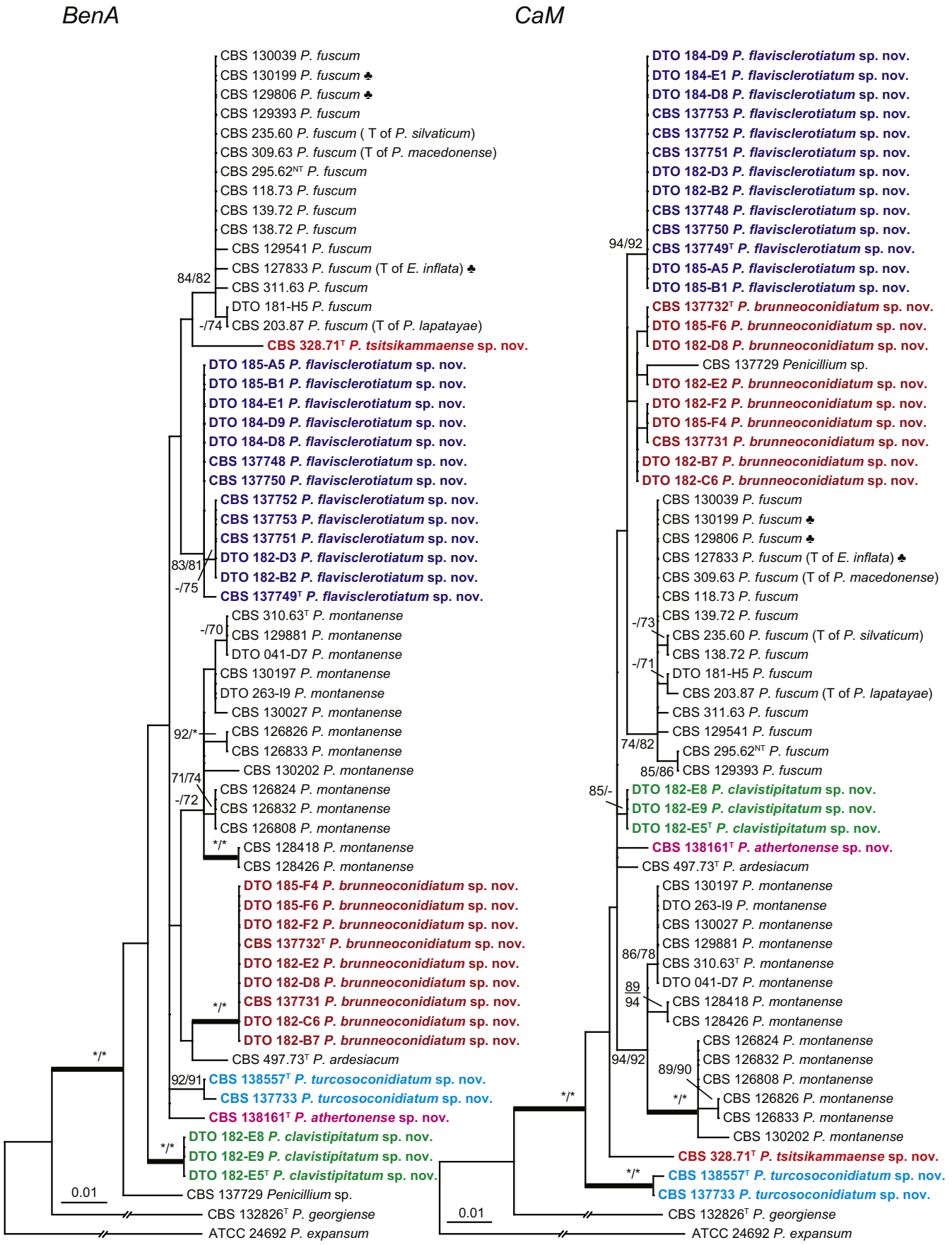

Fig. 12. Phylogenetic trees showing the relationship among strains belonging to the *P. fuscum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

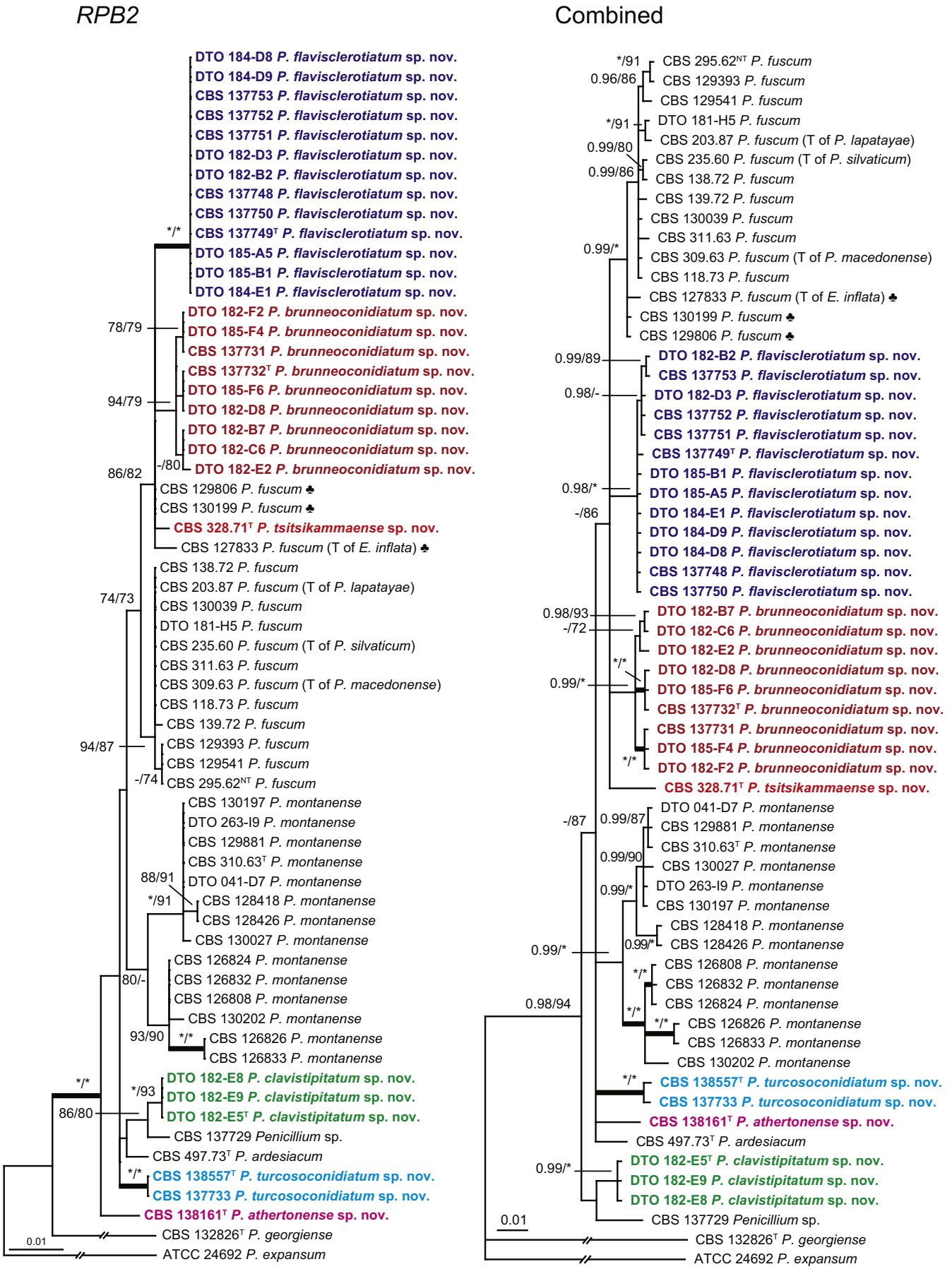

Fig. 13. Phylogenetic trees showing the relationship among strains belonging to the *P. fuscum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

Table 5. Overview of diagnostic characters of species belonging to the *P. fuscum*-clade.

Species name	CYA	MEA	YES	CYA30 °C	Stipe length (µm)	Stipe ornamentation	Conidial size (µm)	Sclerotia/cleistothecia
P. ardesiacum	27–33	32–38	30–40	25–30	75–250	Smooth to finely roughened	2.5–3.5	Absent
P. athertonense	27–31	27–33	27–31	20–25	(30–)60–200	Smooth	3.5–4.0	Absent
P. brunneoconidiatum	18–24	10–17	20–25	(0–)10–18	7.5–30	Smooth	3.5–4.5	Absent
P. clavistipitatum	17–23	20–25	18–27	0–15	20–120	Rough	2.5–3.0	Absent
P. flavisclerotiatum	23–26	23–28	30–35	18–21	20–80	Smooth	2.0–3.5	Sclerotia; yellow
P. fuscum	31–37	30–36	31–37	0–10	15–120	Smooth	2.5–4.0(–5.5)	Cleistothecia; yellow and becoming avellaneous to reddish brown
P. montanense	15–25	20–35	(19–)25–30	(0–)3–13	20–100(–150)	Smooth	Variable: (2.5–)4.0–4.5(–5.5)	Absent
P. tsitsikammaense	10–15	19–23	20–25	5–10	25–50	Smooth	2.7–3.3(–5.5)	Sclerotia[1]; white
P. turcosoconidiatum	15–20	18–25	20–25	7–10	6–30	Smooth	2.0–2.5	Absent

[1] Sclerotia on MEA. Stolk & Samson (1983: 127) reported ascospores in the type strain of *P. tsitsikammaense* (CBS 328.71).

P. saturniforme-clade (76 % ML; 1.00 pp) (Fig. 1). The species of the *P. sublectaticum*-clade are predominantly monoverticillate while those of the latter two clades have a biverticillate branching pattern. Additionally, all isolates of this clade are able to grow on CYA incubated at 30 °C, a feature not observed in the *P. verhagenii* and *P. saturniforme*-clades. Phylogenetic analysis of the individual *BenA*, *CaM* and *RPB2* data sets divided these strains into three well-supported lineages that are described here as new species: *P. infra-aurantiacum*, *P. malmesburiense* and *P. sublectaticum* (Fig. 14). The combined analysis of the *BenA*, *CaM* and *RPB2* genes indicated that *P. sublectaticum* and *P. malmesburiense* are sister species, although with poor statistical support (0.96 pp, <70 % ML) (Fig. 14). Phenotypically, *P. sublectaticum* differs from *P. malmesburiense* in having a pale reverse on CYA, CYAS and DG18, and from *P. infra-aurantiacum* by having irregular margins on CYA and a dark brown reverse on CYA with (yellow) brown margins.

Clade 7: *Penicillium verhagenii*-clade

Isolates belonging to the *P. verhagenii*-clade are phylogenetically most closely related to *P. saturniforme* (Fig. 1; 1.00 pp; 88 % ML), and differ from all species in section *Aspergilloides* by their biverticillate conidiophores. These isolates are characterised by a unique mode of conidiophore development. The conidiophores are initially biverticillate, but can be become divaricate following sympodial branching of the stipe at the apex. Furthermore, the conidia of these species are blue-green or have a blue shade on MEA. Two clades are consistently present in the separate analysis of the *BenA*, *CaM* and *RPB2* sequences and are treated here as the new species *P. verhagenii* and *P. ranomafanaense* (Fig. 15). These two species can be recognised by their reverse colour on CYA, YES and DG18. *Penicillium ranomafanaense* has orange or reddish reverse colours on CYA and YES and smooth to finely roughened conidiophore stipes, while *P. verhagenii* isolates have a yellow or yellow-brown reverse and distinctly rough walled stipes.

Clade 8: *Penicillium saturniforme*-clade

Penicillium saturniforme (CBS 122276^T) occupies a unique and isolated position in the phylogeny of section *Aspergilloides* (Fig. 1). Phylogenetically, it is most closely related to species of the *P. verhagenii*-clade (1.00 pp; 88 % ML). Species of the *P. verhagenii*-clade and *P. saturniforme* are predominantly biverticillate, a unique feature in section *Aspergilloides*. *Penicillium verhagenii* and *P. ranomafanaense* have divaricate conidiophores following secondary, sympodial growth at the apex of the stipe, a feature not reported in *P. saturniforme* (Wang & Zhuang, 2009). Furthermore, *P. saturniforme* produces ascospores and these are not observed in cultures of *P. verhagenii* and *P. ranomafanaense*.

Clade 9: *Penicillium lividum*-clade

The *Penicillium lividum*-clade is most closely related to the *P. hoeksii*-clade (1.00 pp; >95 % ML) and basal to these two clades is the *P. quercetorum*-clade (0.99 pp; 89 % ML). The species of the *P. lividum*-clade produce (dark) blue-green conidia on MEA, grow moderately fast on CYA (25–35 mm) and very poorly on CREA, without the production of acidic compounds. Furthermore, the conidiophores are densely packed with phialides and the conidia are broadly ellipsoidal or ellipsoidal and distinctly roughened, often striate. Most of these characters are shared with *P. hoeksii*. The main differences between both the two clades are the absence of growth of species of the *P. hoeksii*-clade on CYA30°C and the finely roughened conidia produced by *P. hoeksii*.

Fig. 16 shows the phylogenetic relationships among species of the *P. lividum*-clade. Three species are accepted: *P. lividum*, *P. odoratum* and *P. kananaskense*. These species are resolved in well-supported lineages, but the relationship among the species is incongruent in the individual *BenA*, *CaM* and *RPB2* phylogenies. In the *CaM* data set, *P. kananaskense* is a sister species of *P. odoratum*, but with low statistical support (<70 % ML; 73 % MP). In contrast, *P. kananaskense* and *P. lividum* are sister species with high bootstrap support (>95 % in ML and MP) in the *RPB2* analysis.

Penicillium lividum was accepted by Pitt (1980) and *P. odoratum* and *P. trzebinskianum* were regarded as synonyms. Our phylogenies (Fig. 16) place *P. odoratum* in a distinct clade separate from *P. lividum*. *Penicillium trzebinskianum* (CBS 530.93^T) was invalidly described (without a Latin diagnosis) and was subsequently validated by Ramírez (1982). Our data show that this species is a synonym of *P. odoratum*.

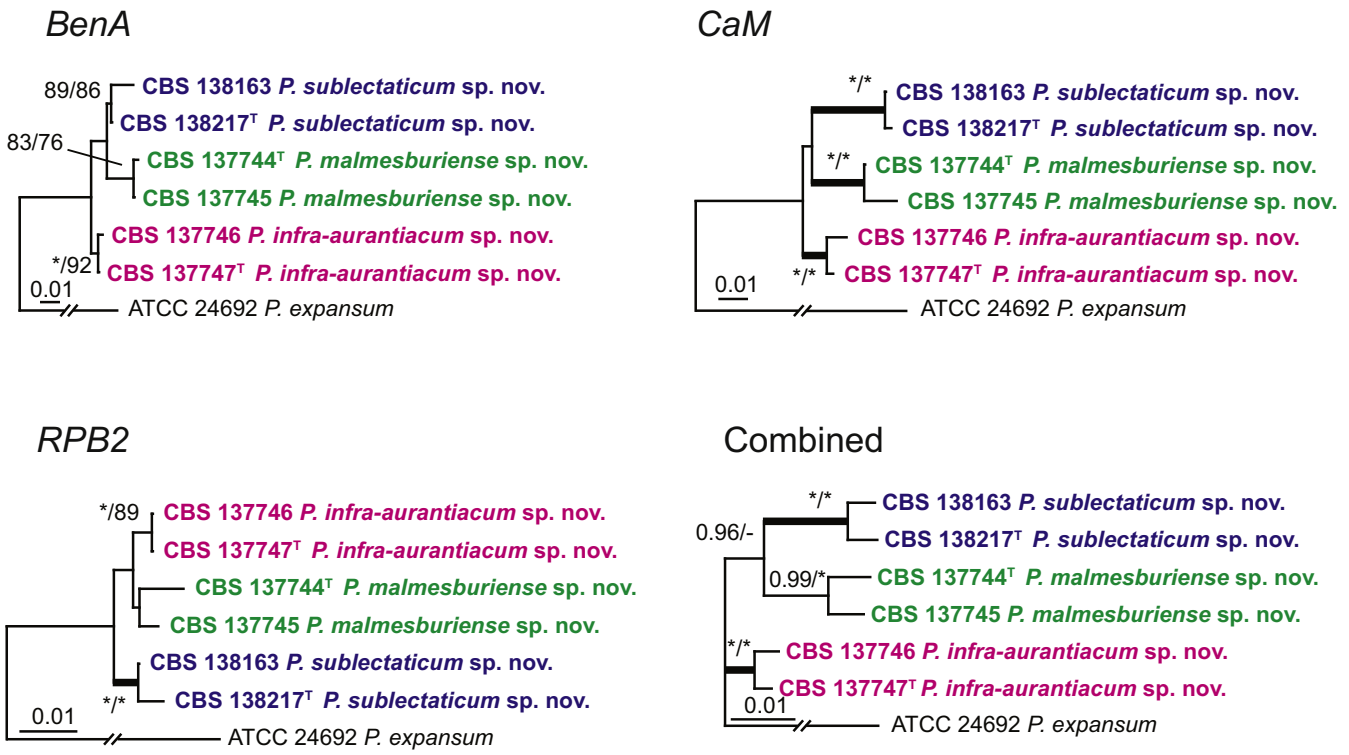

Fig. 14. Phylogenetic trees showing the relationship among strains belonging to the *P. sublectaticum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

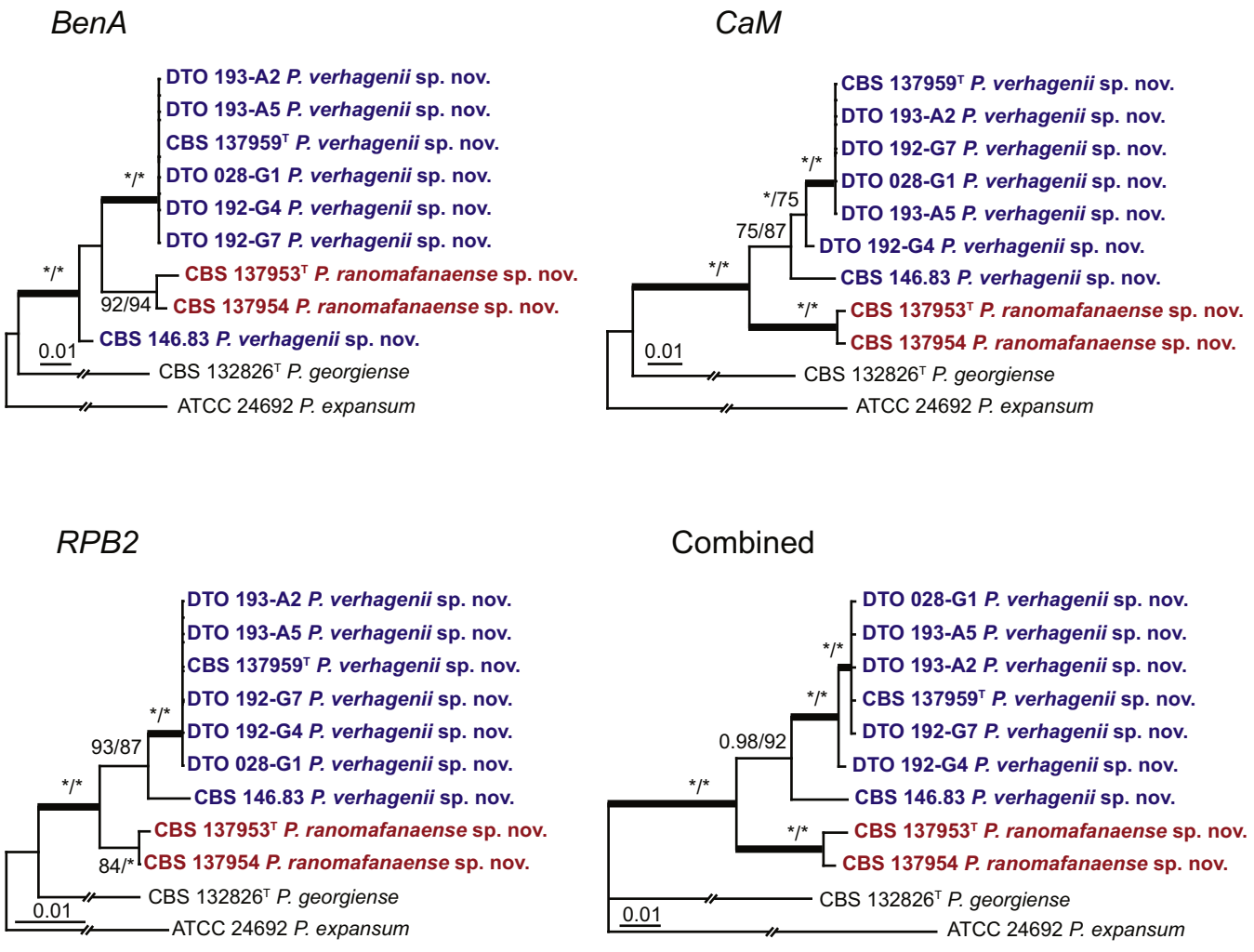

Fig. 15. Phylogenetic trees showing the relationship among strains belonging to the *P. verhagenii*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

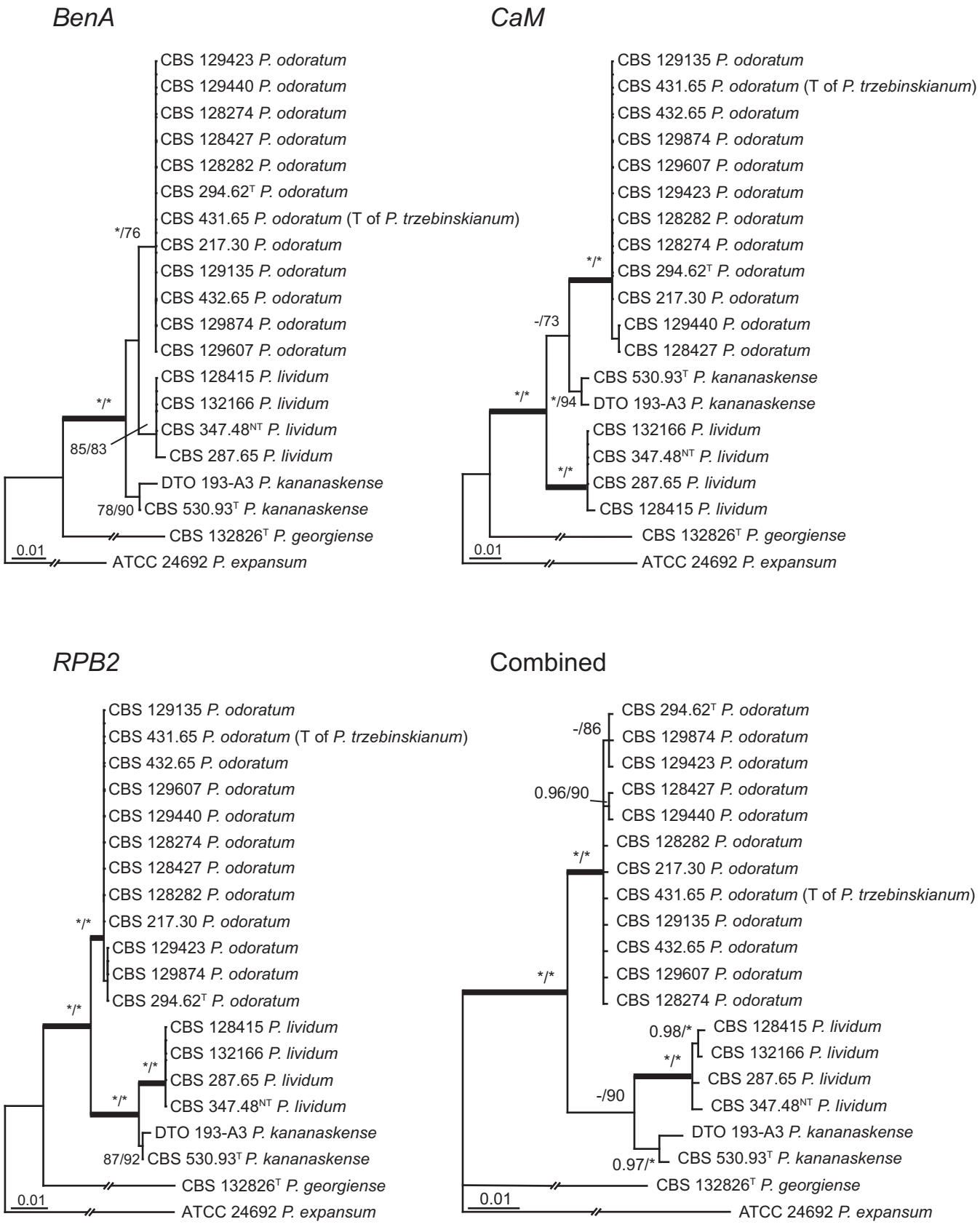

Fig. 16. Phylogenetic trees showing the relationship among strains belonging to the *P. lividum*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

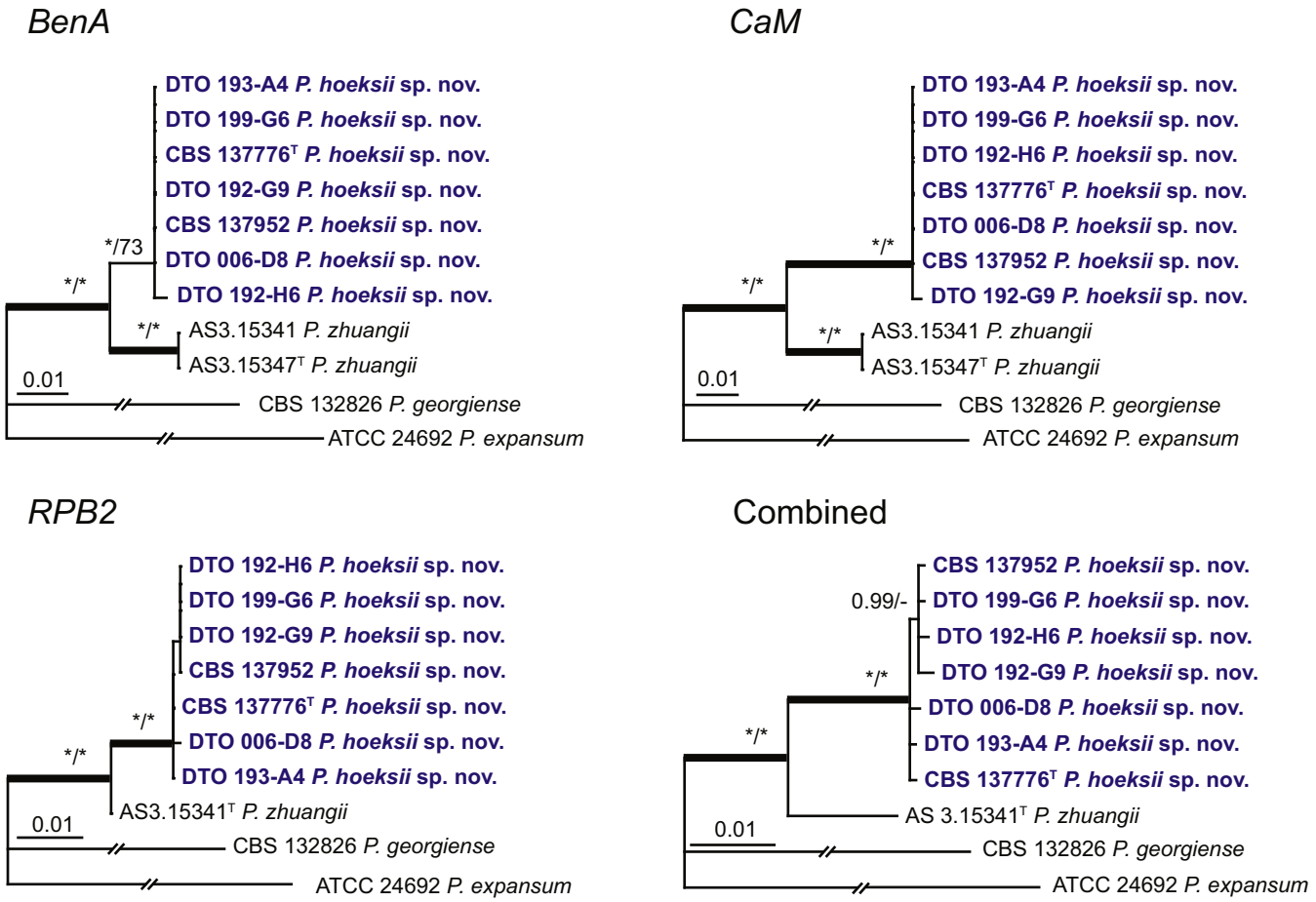

Fig. 17. Phylogenetic trees showing the relationship among strains belonging to the *P. hoeksii*-clade. The bar indicates the number of substitutions per site. The phylogram is rooted with *P. expansum* (ATCC 24692).

Penicillium kananaskense (CBS 530.93^{T}) was described as a pink-spored *Penicillium* species (Seifert *et al.* 1994). An additional strain of this species was examined (DTO 193-A3), which produced dark blue-green conidia on MEA. Although CBS 530.93^{T} and DTO 193-A3 differ in conidial colour, they share some characters that are not observed in other species of the *P. lividum*-clade. For example, both strains grow slowly on CYA30°C (5–10 mm) and have a vivid yellow or orange reverse on CYA and YES with yellow pigments diffusing into the agar. *Penicillium odoratum* grows well on CYA30°C (28–35 mm) while *P. lividum* grows slowly (12–17 mm). The reverse colours on CYA and YES between these two species are similar (pale, beige, pale brown). The colony texture could also be used to distinguish these three species. *Penicillium kananaskense* produces velvety colonies on MEA, *P. odoratum* floccose colonies and the colonies of *P. lividum* have a lanose texture.

Clade 10: *Penicillium hoeksii*-clade

Seven strains (DTO 006-D8; DTO 068-D9; DTO 192-G9; CBS 137776^{T}, DTO 192-H6; DTO 193-A4; DTO 199-G6) clustered together in our survey of section *Aspergilloides* isolates. Fig. 1 shows that two representatives of this group included in this analysis (DTO 068-D9, CBS 137776^{T}) form a distinct clade within section *Aspergilloides*. This unique clade, here named the *P. hoeksii*-clade, is closely related to the *P. lividum*- and *P. quercetorum*-clades (Fig. 1; 0.99 pp; 89 % ML). Species of the *P. hoeksii*-clade differ from those of the *P. lividum*-clade by shorter stipes (less than 250 µm), which are smooth-walled. The recently described *P. zhuangii* belongs to the *P. hoeksii*-clade (Wang *et al.* 2014). Our set of isolates is phylogenetically (Fig. 17) and phenotypically distinct from *P. zhuangii*. We therefore describe this set of seven isolates as a new species, *P hoeksii*. Phenotypically, *P. hoeksii* and *P. zhuangii* share features such as moderate growth on CYA (15–28 mm), absence of growth on CYA incubated at 30 °C and the production of (broadly) ellipsoidal conidia. The species differ mainly in their response to temperatures. *Penicillium zhuangii* grows faster on CYA incubated at 15 °C than on 25 °C (22–24 *vs* 15–18 mm), while *P. hoeksii* isolates grow slower at 15 °C (12–18 mm *vs* 20–28 mm).

Clade 11: *Penicillium quercetorum*-clade

Penicillium quercetorum is the only species of the *P. quercetorum*-clade. Pitt (1980) noted similarities between *P. quercetorum* and *P. thomii*, but accepted *P. quercetorum* based on a slower growth, smooth walled stipes and spheroidal rather than ellipsoidal conidia. However, in other studies, this species was placed in synonymy with *P. thomii* (Ramírez 1982, Pitt *et al.* 2000). Our data show that this species is phylogenetically related to the *P. hoeksii*- and *P. lividum*-clades (Fig. 1; 0.99 pp; 89 % BS) and more distant from the *P. thomii*-clade.

Table 6. Overview of ITS sequences types of section *Aspergilloides* species. The GenBank numbers and haplotype numbers in bold font are shared among other species, and those in regular font are species specific. The species in pale yellow can be identified based on ITS sequences only, species in olive green share sequences with other *Aspergilloides* members.

No.	Species	GenBank no. ITS sequences	Haplotype number (number of isolates per haplotype)
1	*P. ardesiacum*	KM189565	47 (1)
2	*P. armarii*	KM189758	24 (3)
3	*P. athertonense*	**KM189462**	**49 (1)**
4	*P. aurantioviolaceum*	**KM189552**	**23 (1)**
5	*P. austroafricanum*	KM189610, **KM189637**	25 (4), **26 (3)**
6	*P. brunneoconidiatum*	KM189663, KM189666, KM189665, **KM189691**	40 (1), 42 (2), 43 (1), **49 (4)**
7	*P. bussumense*	**KM189458**	**30 (1)**
8	*P. cartierense*	**KM189557**	**23 (2)**
9a	*P. clavistipitatum*	KM189667	39 (3)
9b	*P. clavistipitatum* cf.	KM189654	37 (1)
10	*P. contaminatum*	**KM189575**	**23 (2)**
11	*P. crocicola*	**KM189768**	**26 (9)**
12	*P. flavisclerotiatum*	KM189671	41 (6), 48 (7)
13	*P. frequentans*	**KM189762**	**30 (19)**
14	*P. fuscum*	KM189547, KM189567	12 (16), 46 (1)
15	*P. fusisporum*	**KM189757**	**23 (3)**
16	*P. glabrum*	KM189732, KM189764, KM189619, KM189455**, KM189631**	27 (1), 28 (1), 29 (7), **30 (59)**, **31 (1)**
17	*P. grancanariae*	**KM189529**	**21 (1)**
18	*P. grevilleicola*	**KM189630**	**18 (2)**
19	*P. hoeksii*	KM189523	13 (2)
20	*P. infa-aurantiacum*	**KM189650**, KM189684	**4 (1)**, 5 (1)
21	*P. jejuense*	KM189623, **KM189678**	16 (1), **18 (1)**
22	*P. kananaskense*	**KM189780**	**11 (2)**
23	*P. kiamaense*	**KM189506**	**19 (1)**
24	*P. lividum*	**KM189582**	**11 (4)**
25	*P. longicatenatum*	KM189751, KM189627, KM189636, KM189633	32 (1), 33 (10), 34 (7), 35 (1)
26	*P. malmesburiense*	**KM189676**	**5 (2)**
27	*P. montanense*	KM189715, **KM189722**	44 (1), **49 (13)**
28	*P. odoratum*	**KM189796**	**11 (10)**
29	*P. palmense*	**KM189528**	**21 (1)**
30	*P. pulvis*	KM189640, **KM189632**	30 (2), **31 (1)**
31	*P. purpurescens*	**KM189561**	**23 (2)**
32	*P. quercetorum*	KM189556	36 (2)
33	*P. ranomafanaense*	KM089553, KM189541	7 (1), 10 (1)
34	*P. roseomaculatum*	KM189466, KM189535, KM189465, **KM189490**	14 (1), 15 (1), 17 (1), **18 (7)**
35	*P. roseoviride*	**KM189549**	**23 (1)**
36	*P. rudallense*	**KM189638**	**23 (5)**
37	*P. saturniforme*	KM189585	2 (1)
38	*P. spinulosum*	**KM189781**	**18 (15)**
39	*P. sterculiniicola*	**KM189754**	**18 (5)**
40	*P. sublectaticum*	KM189527	3 (2)
41	*P. subspinulosum*	KM189509, KM189741	20 (2), 22 (20)
42	*P. thiersii*	KM189474	1 (1)
43	*P. thomii*	**KM189473**	**23 (7)**
44	*P. trzebinskii*	**KM189799**	**21 (11)**
45	*P. tsitsikammaense*	KM189451	45 (1)
46	*P. turcosoconidiatum*	KM189645, **KM189646**	38 (1), **49 (1)**
47	*P. vagum*	**KM189572, KM189590, KM189475**	**18 (5), 19 (16), 49 (1)**
48	*P. valentinum*	**KM189731**	**23 (4)**
49	*P. verhagenii*	KM189461, KM189704, KM189460	6 (1), 8 (5), 9 (1)
50	*P. yezoense*	**KM189554**	**23 (13)**
51	*P. zhuangii*	KF769435	50 (2)

Clade 12: *Penicillium thiersii*-clade

Based on a four gene phylogeny, *P. thiersii* was convincingly placed in section *Aspergilloides* by Houbraken & Samson (2011). The phylogenetic placement of this species within section *Aspergilloides* could not be confirmed in our study because of a lack of statistical support (Fig. 1). *Penicillium thiersii* is resolved on its own, basal to other species of section *Aspergilloides*. The long, vesiculate, rough-walled stipes and ellipsoidal conidia suggest a relationship with species of the *P. thomii*-clade. In contrast, *P. thiersii* has a slower growth rate than species of the *P. thomii*-clade (Peterson *et al.* 2004). No sclerotia or cleistothecia were reported in the original description of *P. thiersii*. However, macro- and microscopic examination of CBS 117503^T showed presence of pale brown cleistothecia on MEA, CYA and DG18. The ascospores of *P. thiersii* are ellipsoidal, measure 1.7–2.5 × 2.5–3.5 µm, and have an equatorial ridge and smooth to finely roughened valves. *P. thiersii* produce a series of different extrolites, making it chemically very distinctive: thiersinines, thiersindoles, decaturins and oxalicins (Li *et al.* 2002, 2003, 2005).

ITS barcoding and identification

The ITS locus is the accepted barcode for fungal identification (Schoch *et al.* 2012). Sixteen of 51 *Aspergilloides* species (31.3 %) could be identified using ITS sequences and therefore this locus cannot be used alone for species level identification in this group. This confirms previously published data on the use of the ITS barcodes for species recognition in *Penicillium* (e.g. Skouboe *et al.* 1999, Houbraken *et al.* 2011b, 2012a, b).

ITS sequences were generated from the majority of the strains used in the phylogenies described above. Fifty haplotypes were detected among the 365 investigated ITS sequences. An overview of the various haplotypes is given in Table 6. Fifteen species did not share ITS sequences with other species of sect. *Aspergilloides*. Among those fifteen species were *P. longicatenatum*, *P. hoeksii*, *P. quercetorum*, *P. saturniforme* and *P. thiersii*, species that were also phylogenetically very distinct (Fig. 1). *Penicillium ardesiacum* and *P. tsitsikammaense* were represented by only one strain and multiple strains of *P. ranomafanaense* and *P. armarii* were included in the analysis; however, these strains were isolated from the same substrate and location. We speculate that these species might also share ITS sequences with other species of sect. *Aspergilloides* when a more diverse set of isolates can be analysed. Interestingly, the investigated *P. subspinulosum* isolates had unique ITS sequences, although the species is closely related to *P. roseomaculatum*, *P. trzebinskii* and *P. spinulosum* in our analyses of the *BenA*, *CaM* and *RPB2* genes. *Penicillium trzebinskii* could also be distinguished from those species based on its ITS barcode; however, this species also shared sequences with the phenotypically distinct *P. grancanariae* and *P. palmense*.

Some haplotypes were predominantly present. Haplotype 11 contained only species of the *P. lividum*-clade and none of *P. lividum*-clade species belonged to another haplotype. With the exception of *P. crocicola* and *P. austroafricanum*, all *P. thomii*-clade species are represented by haplotype 18 and 23. However, these haplotypes do not exclusively accommodate *P. thomii*-clade species and can therefore not be used for "clade" level identification. Other *P. thomii*-clade species have haplotypes 25 (*P. austroafricanum*) and 26 (*P. austroafricanum* and *P. crocicola*). Eighty-one isolates have haplotype 30. All *P. frequentans* and the majority of *P. glabrum* share this haplotype. The only other species with this haplotype is *P. pulvis* (two of the three examined sequences).

BenA is recommended as a general purpose secondary barcode for precise species identification in *Penicillium* (Samson *et al.* 2010, Visagie *et al.* 2014). Either partial *CaM*, *BenA* and *RPB2* sequences can be used for identification purposes in section *Aspergilloides* and all sequences obtained were species specific. The use of *BenA* might be hampered by a high intra-specific variation in *P. glabrum* (4.0 %) and *P. frequentans* (3.0 %). It is unclear whether this variation is only present in these two species. Perhaps it occurs in other species of sect. *Aspergilloides*, but we may not have observed it because of our limited sample size. Alternatively, it is feasible that there are additional phylogenetic species, or incipient speciation, in *P. glabrum* and *P. frequentans* that are only hinted at by our data. The difficulties of correct identification linked to a high intra-specific variation will be solved by continued sampling of *BenA* sequences to assay intra-species diversity, leading to higher similarity matches.

Phenotypic and physiologic characters can be used for species identification. Although there are differences in phenotype, identification based on these features remains difficult for non-specialists and a sequence-based approach is recommended, followed by assessment of confirmatory phenotypic characters. Various factors can hinder a phenotype-based identification, including lab-to-lab or batch-to-batch differences in agar media, degeneration of strains and subjective interpretation of structures and colours. If only a phenotype-based identification is possible, then it is of major importance to follow the recommendations listed in Visagie *et al.* 2014.

TAXONOMY

Our phylogenetic analysis revealed that section *Aspergilloides* currently contains 51 species. The 26 new species that belong to this section are described below.

Penicillium armarii Houbraken, Visagie, Samson & Seifert, **sp. nov.** MycoBank MB809955. Fig. 18.

Etymology: Named after the collection site, in a closet.

Diagnosis: This species belongs to the *P. glabrum*-clade and can be differentiated by its fast growth rate on CYA (25 and 30 °C) and MEA, and good growth on CREA.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium glabrum*-clade.

Typus: **Australia**, Tasmania, Hobart, house dust, collected by G. Gates, 2009, isolated by E. Whitfield and K. Mwange (holotype CBS H-21870, culture ex-type CBS 138171 = DTO 235-F1).

Barcode and molecular based ID: ITS barcode: KM189758 (alternative markers: *BenA* = KM089007; *CaM* = KM089394; *RPB2* = KM089781).

Description: Colony diam, 7 d, in mm: CYA 50–56 CYA15°C 25–31; CYA30°C 46–52; CYA37°C no growth; MEA 54–60; YES 51–57; DG18 34–40; CYAS 31–37; ratio CYAS:CYA

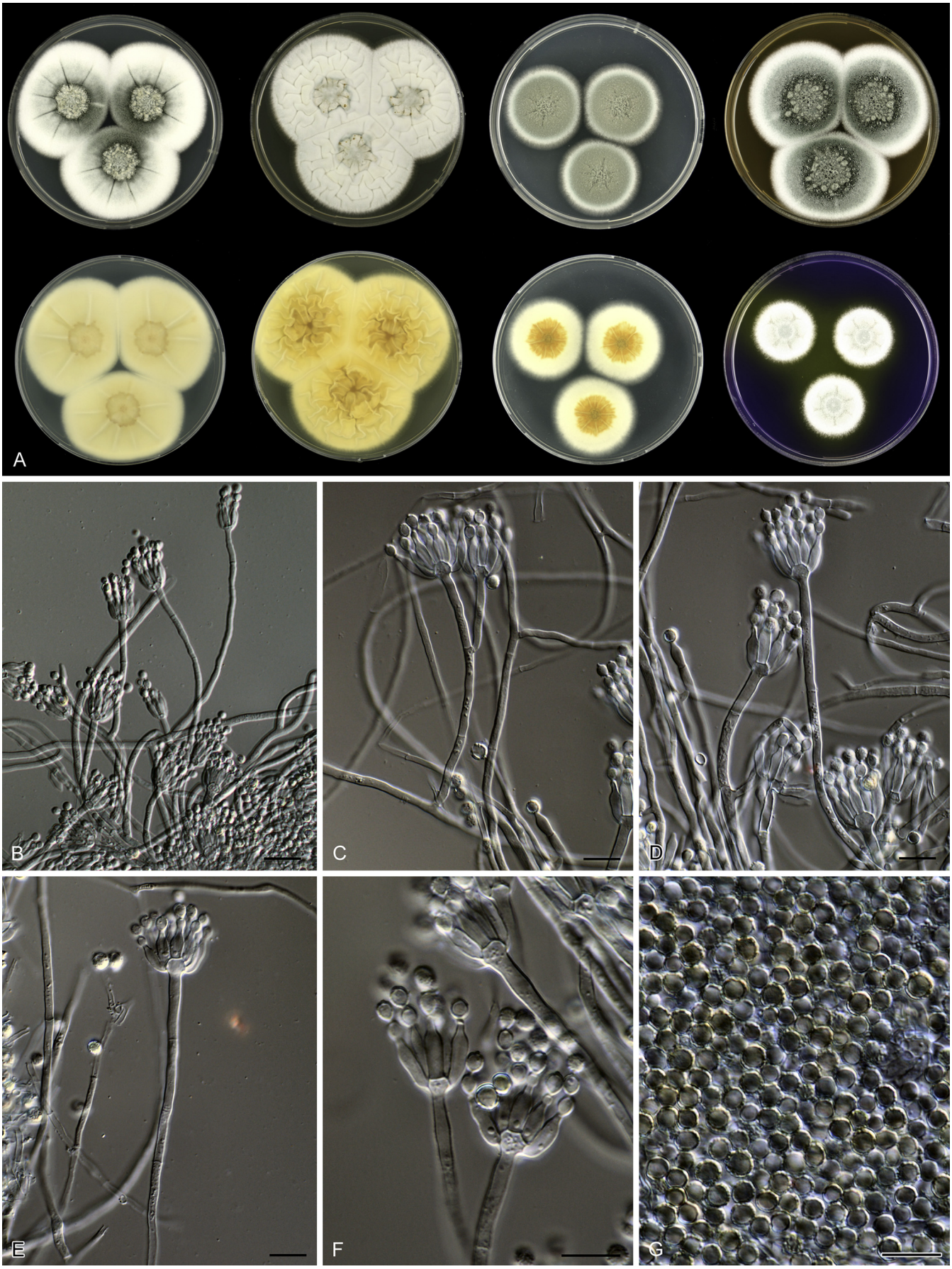

Fig. 18. *Penicillium armarii*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

0.60–0.70; CREA 25–31, good growth, moderate acid production, followed by base production.

Sporulation on CYA moderate to good, colony texture weakly floccose, light radially sulcate; conidia dark dull green; mycelium inconspicuous; exudate present in the centre as large clear exudate droplets; soluble pigments absent; margin entire; reverse pale yellow. Sporulation on YES absent or very poor, mycelium white; soluble pigments absent; reverse yellow with orange centre. Good sporulation on DG18, colony texture crustose; conidia dull green; reverse pale with orange-brown centre. Good sporulation on MEA, colony texture floccose; conidia dark green in the centre, dull green toward the edge; exudate present as large clear droplets; reverse colour not affecting medium. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 50–300 µm long, apices vesiculate, especially in older parts of the colony, up to 5.5 µm, smooth walled, predominantly monoverticillate, sometimes with divergent additional branch up to 15 µm long, stipe 2.0–3.5 µm wide. Phialides ampulliform with distinct neck, 6–14 per stipe, 8.5–10.5 × 2.5–3.0 µm. Conidia in long distorted chains, globose, distinctly ornamented 3.2–4.0 µm diam.

Penicillium athertonense Houbraken, **sp. nov.** MycoBank MB809956. Fig. 19.

Etymology: Referring to Atherton Tablelands, the location of the type strain.

Diagnosis: The species is phylogenetically distinct from other species of the *P. fuscum*-clade. Phenotypically, it can be distinguished by a fast growth rate on CYA at 30 °C (20–25 mm).

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium fuscum*-clade.

Typus: **Australia**, Queensland, Atherton Tableland, forest soil, isolated by J. Houbraken & R. van Leeuwen (holotype CBS H-21874, culture ex-type CBS 138161 = DTO 030-C2).

Barcode and molecular based ID: ITS barcode: KM189462 (alternative markers: *BenA* = KM088690; *CaM* = KM089075; *RPB2* = KM089462).

Description: Colony diam, 7 d, in mm: CYA 27–31; CYA15°C 9–13; CYA30°C 20–25; CYA37°C no growth; MEA 27–33; YES 27–31; DG18 17–21; CYAS 15–20; ratio CYAS:CYA 0.6–0.65; CREA 8–12, weak growth and no acid production.

Sporulation on CYA strong; colony texture velvety, radially sulcate, low; conidia dark green; mycelium white; exudate absent; soluble pigment not produced; margin entire; reverse pale yellow to yellow in colony centre, pale beige at the margin. Sporulation on YES poor, conidia pale green; mycelium white; soluble pigment not produced; reverse pale yellow. Moderate to good sporulation on DG18, colony texture velvety; conidia dark green in the centre, dull blue-green on the edge of colony; mycelium white; reverse pale. Sporulation on MEA moderate to good; colony texture velvety; conidia pure (dark) green; exudate present as small, pale droplets; reverse centre brown, reverse of not affecting; Ehrlich reaction negative.

Sclerotia absent. Conidiophores, (30–)60–200 µm long, smooth walled; slightly vesiculate up to 5 µm wide; frequently with an additional branch, 13–19 µm long. Phialides divergently arranged, widest above the middle and with a short neck, 4–14 per stipe, 8.0–9.0 × 2.5–3.0 µm. Conidia in long distorted chains, globose, distinctly roughened, spinose, 3.5–4.0 µm diam.

Penicillium austroafricanum Houbraken & Visagie, **sp. nov.** MycoBank MB809957. Fig. 20.

Etymology: Named after South Africa, the origin of the type strain.

Diagnosis: This species is phylogenetically related to *P. crocicola* and both species have a strong acid production on CREA. *Penicillium austroafricanum* has a pale yellow or pale brown reverse colour on DG18, while *P. crocicola* has a pale or a pinkish-brown reverse colour.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium thomii*-clade.

Typus: **South Africa**, Western Cape, Harold Porter Botanical Garden, leaf of *Phaenocoma prolifera*, isolated by J. Houbraken & P. Crous (holotype CBS H-21864, culture ex-type CBS 137773 = DTO 133-G5).

Barcode and molecular based ID: ITS barcode: KM189610 (alternative markers: *BenA* = KM088854; *CaM* = KM089241; *RPB2* = KM089628).

Description: Colony diam, 7 d, in mm: CYA 51–62; CYA15°C 23–35; CYA30 °C 30–50; CYA37°C no growth; MEA 40–55; YES 45–55; DG18 27–45; CYAS 35–42; ratio CYAS:CYA 0.67–0.77; CREA 30–35, poor growth, strong acid and no base production.

Sporulation on CYA moderately dense to dense; conidia dull green to greyish green, colony texture velutinous and floccose, low, sulcate, creamish sclerotia produced; mycelium white; exudate clear, sometimes absent; soluble pigment not produced; margin low, wide, entire; reverse greenish white to light yellow to light brown, more yellowish in some isolates. Sporulation on YES moderately dense; conidia dull green, colony texture velutinous, moderately deep, sulcate, greyish colour in non-sporulating areas; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse light yellow to dull yellow greyish yellow. Sporulation on DG18 strong; conidia dull green to greyish green, colony texture velvety or floccose, low; mycelium white; exudate absent; soluble pigment not produced; reverse pale yellow, pale brown, greenish white. Sporulation on MEA moderately dense to dense; conidia dull green to greyish green, colony texture velutinous, low, plane, creamish sclerotia produced; mycelium white; exudate clear; soluble pigment not produced; margin low, wide, entire; reverse brownish yellow to yellowish brown. Ehrlich reaction negative.

Sclerotia on MEA, hard, consisting of polygonal cells, 200–400 × 150–250 µm. Conidiophores monoverticillate; stipes distinctly roughened, 45–220 × 2–3.5 µm, vesicles 4–7.5 µm diam. Phialides 13–24 per stipe, ampulliform, 8–10.5 × 2.5–3.5 µm. Conidia smooth to finely rough walled, broadly ellipsoidal or ellipsoidal, 2.5–4 × 2.5–3 µm.

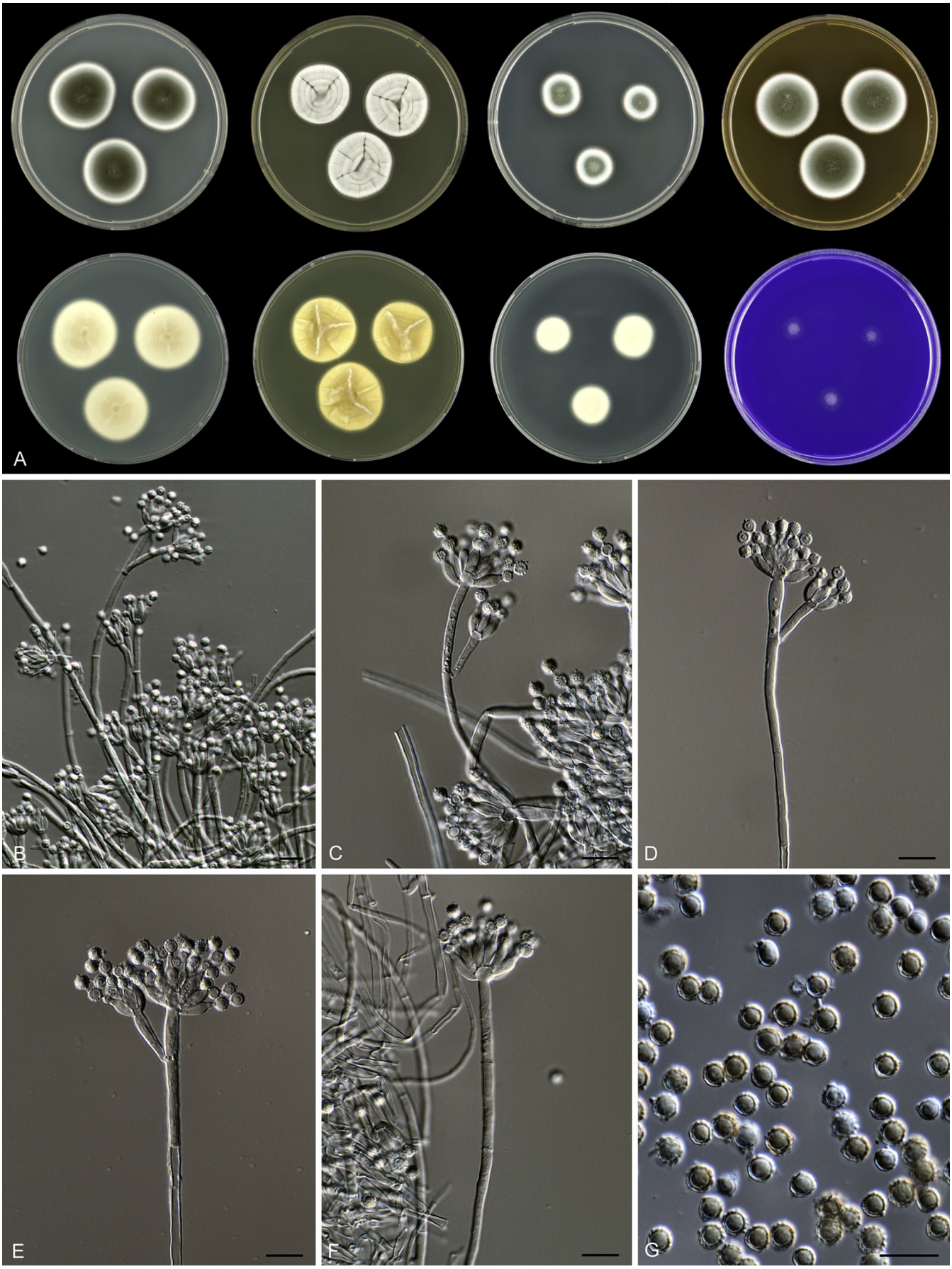

Fig. 19. *Penicillium athertonense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

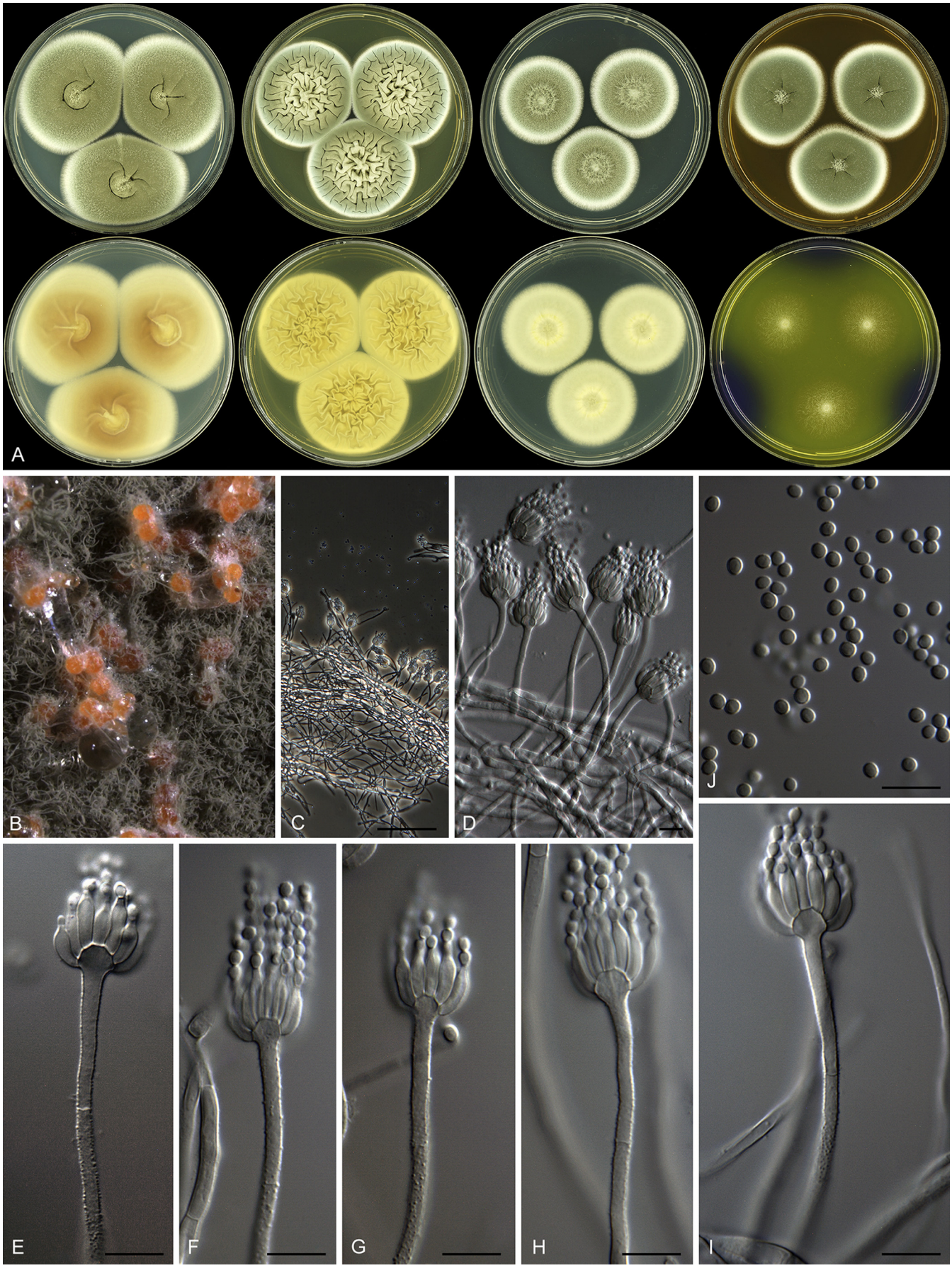

Fig. 20. *Penicillium austroafricanum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B, C. Sclerotia. D–I. Conidiophores. J. Conidia. Scale bars = 10 µm.

Penicillium brunneoconidiatum Visagie, Houbraken & K. Jacobs, **sp. nov.** MycoBank MB809958. Fig. 21.

Etymology: Referring to the brown conidia of the species.

Diagnosis: *Penicillium brunneoconidiatum* differs from the other species belonging to the *P. fuscum*-clade by its restricted growth on CYA, YES and MEA, short stipes, large conidia (3.5–4.5 µm) and dark green to olive green conidia that become dark brown with age (Table 5).

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium fuscum*-clade.

Typus: **South Africa**, Western Cape, Malmesbury, Riverlands, Fynbos, soil, isolated by C.M. Visagie (holotype CBS H-21873, culture ex-type CBS 137732 = DTO 182-E4 = CV 949 = DAOM 241359).

Barcode and molecular based ID: ITS barcode: KM189666 (alternative markers: *BenA* = KM088911; *CaM* = KM089298; *RPB2* = KM089685).

Description: Colony diam, 7 d, in mm: CYA 18–24; CYA15°C 7–15; CYA30°C (0–)10–18; CYA37°C no growth; MEA 10–17; YES 20–25; DG18 21–24; CYAS 6–10; ratio CYAS:CYA 0.3–0.4; CREA 3–6, weak growth, no acid production.

Sporulation on CYA moderately dense to dense; conidia dull green to dark green, becoming brown with age, colony texture velutinous, low to moderately deep, plane to slightly sulcate in some strains; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to greyish green to dull green. Sporulation on YES absent to sparse; conidia greenish white, colony texture floccose, deep, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse pale yellow to light yellow to olive. Sporulation on DG18 absent to sparse; conidia greenish white, colony texture velutinous, low, slightly sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to greyish yellow. Sporulation on MEA dense; conidia dull green, becoming brown with age, colony texture velutinous, moderately deep, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish brown. Ehrlich reaction negative.

Conidiophores monoverticillate; stipes smooth walled, 7.5–30 × 1.5–2.5 µm, with a minor proportion up to 120 µm long, vesicles 2.5–5 µm diam. Phialides ampulliform, 3–6 per stipe, 5–7.5 × 2.5–3.5 µm. Conidia thick and rough walled, globose, 3.5–4.5 µm.

Penicillium bussumense Houbraken, **sp. nov.** MycoBank MB809959. Fig. 22.

Etymology: Referring to Bussum, the location of the type strain.

Diagnosis: This species belongs to the *P. glabrum*-clade and can be differentiated by its CYAS:CYA ratio between 0.99–1.02 and the production of dark green conidia, floccose colonies and with the broad non-sporulating margin on MEA.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium glabrum*-clade.

Typus: **the Netherlands**, Bussum, Spanderswoud, soil, isolated by J. Houbraken (holotype CBS H-21869, culture ex-type CBS 138160 = DTO 018-B2).

Barcode and molecular based ID: ITS barcode: KM189458 (alternative markers: *BenA* = KM088685; *CaM* = KM089070; *RPB2* = KM089457).

Description: Colony diam, 7 d, in mm: CYA 31–37; CYA15°C 22–26; CYA30°C 15–20; CYA37°C no growth; MEA 38–44; YES 40–45; DG18 30–35; CYAS 34–39; ratio CYAS:CYA 0.95–1.05; CREA 18–23, poor growth, weak acid production.

Sporulation on CYA absent; radially sulcate, deep; mycelium white; exudate sparsely produced as yellow droplets; soluble pigments present, weak, yellow-brown; margin entire; reverse pale beige at the margin, dark brown in the centre. Sporulation on YES poor; conidia pale grey-green; mycelium white; soluble pigments absent; reverse yellow-brown. Good sporulation on DG18, colony texture velvety; conidia dark green; reverse pale in the centre, transparent at the margin. Good sporulation on MEA, colony texture floccose; conidia dark green; exudate present as small clear droplets; reverse colour not affecting medium. Ehrlich reaction negative.

Sclerotia absent. Conidiophores short, 50–250 µm long, stipes vesiculate up to 5.5 µm diam, finely to distinctly rough-walled, predominantly monoverticillate, sometimes with divergent additional branch up to 20 µm long, stipe 2.5–3.5 µm wide. Phialides ampulliform, densely packed, 6–20 per stipe, 8.0–10.0 × 2.5–3.0 µm. Conidia in long distorted chains, globose, finely ornamented, 2.7–3.2 µm diam.

Penicillium cartierense Houbraken, **sp. nov.** MycoBank MB809960. Fig. 23.

Etymology: Named after Cartierheide, the Netherlands, origin of the type strain.

Diagnosis: The species is phylogenetically unique and similar to other species of the *P. thomii*-clade, differing by the production of reddish brown sclerotia.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium thomii*-clade.

Typus: **the Netherlands**, Eersel, Cartierhiede, soil, isolated by J. Houbraken (holotype CBS H-21861, culture ex-type CBS 137956 = DTO 092-H9).

Barcode and molecular based ID: ITS barcode: KM189564 (alternative markers: *BenA* = KM088804; *CaM* = KM089189; *RPB2* = KM089576).

Description: Colony diam, 7 d, in mm: CYA 42–49; CYA15°C 23–29; CYA30°C 17–32; CYA37°C no growth; MEA 46–50; YES 51–55; DG18 28–34; CYAS 30–37; ratio CYAS:CYA 0.66–0.81; CREA 13–19, weak growth and no or very poor acid production.

Weak sporulation on CYA and only in the centre; colony texture floccose, radial sulcate; conidia pale dull green or dull green; mycelium white; exudate absent or present as small pale yellow

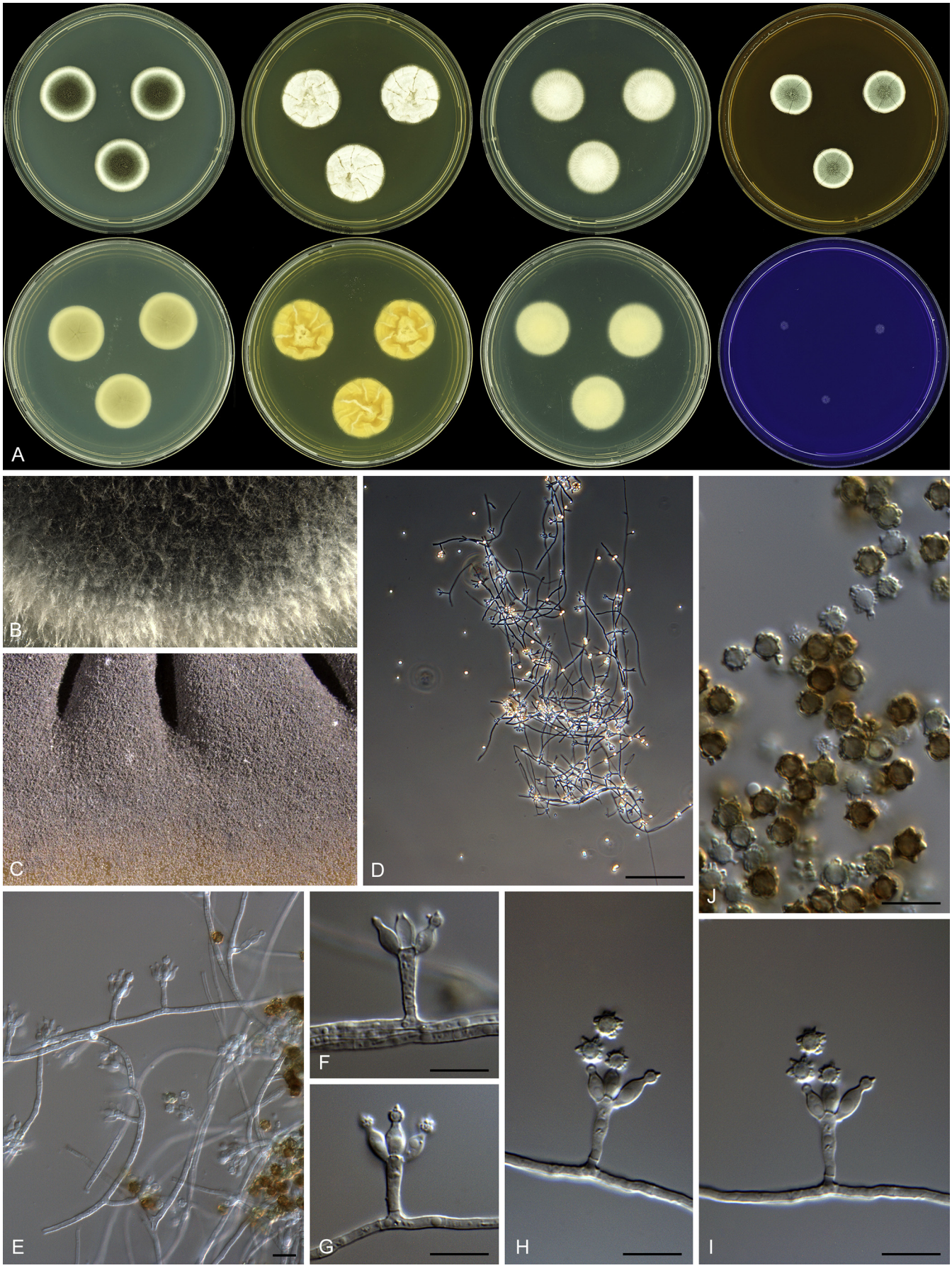

Fig. 21. *Penicillium brunneoconidiatum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B, C. Colony texture. D–I. Conidiophores. J. Conidia. Scale bars = 10 µm.

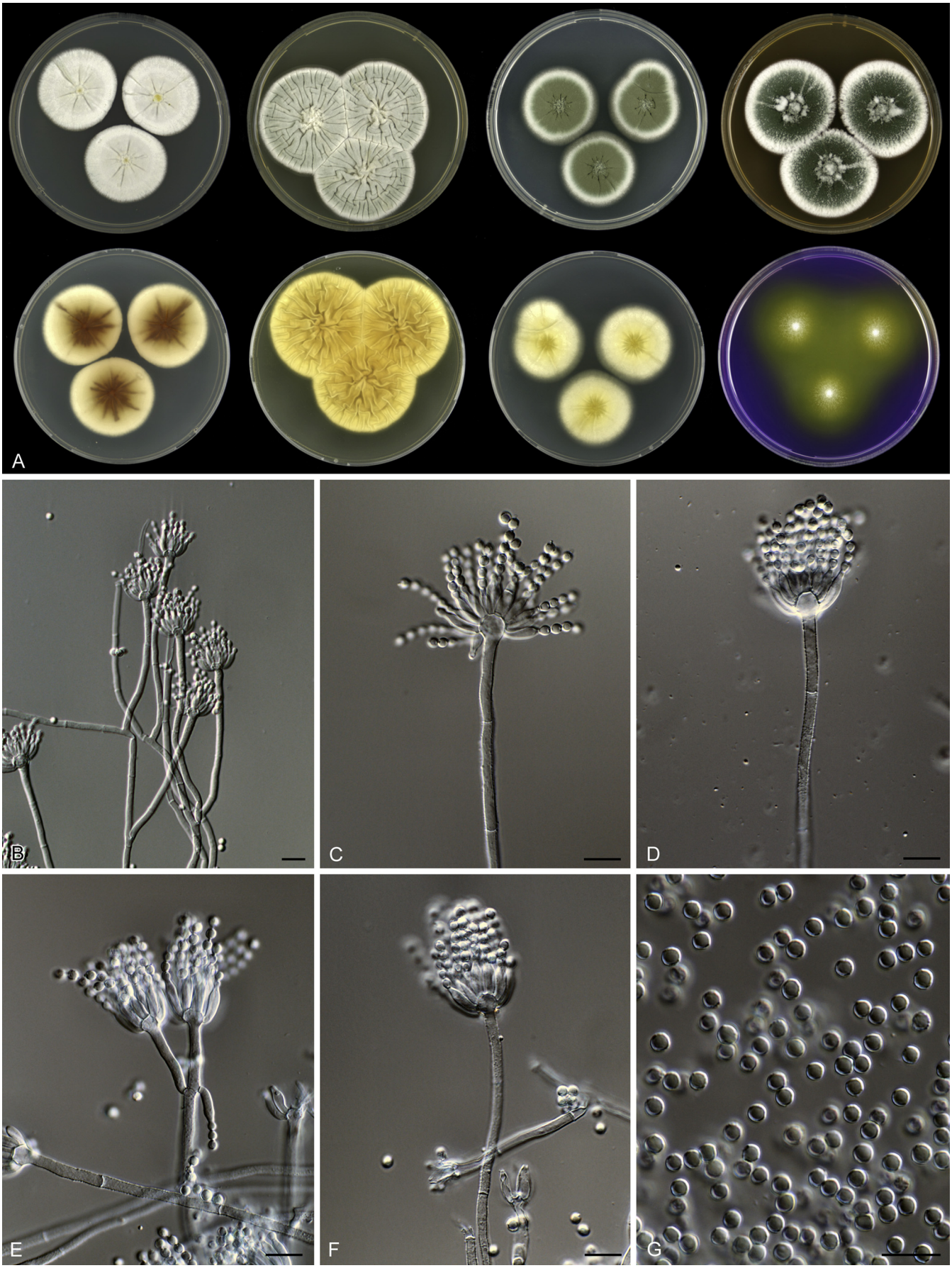

Fig. 22. *Penicillium bussumense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Fig. 23. *Penicillium cartierense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–C, F. Sclerotia. D–E, G. Conidiophores. H. Conidia. Scale bars = 10 µm.

droplets; soluble pigments absent; margin entire; reverse pale brown with dark brown centre becoming reddish brown in time (CBS 863.71). Sporulation on YES absent or poor, conidia dull grey green; mycelium white or very pale crème; soluble pigments absent; reverse yellow-brown. Strong sporulation on DG18, conidia dull green; reverse pale to pale brown or yellow-brown. Moderate to good sporulation on MEA, colony texture floccose; conidia dull green; sclerotia abundantly present, pale brown when young becoming red-brown at age; exudate present as large, clear to light brown droplets; colony reverse yellow in centre, colour medium under colony margins not affected. Ehrlich reaction negative.

Sclerotia pale brown when young, becoming reddish brown after three weeks of incubation at RT on MEA, 250–500(–650) µm; hard; consisting of polygonal cells; no asci or ascospores observed. Conidiophores 150–250 µm long, vesicles 4–7 µm diam, (finely) roughened with ornamentation up to apex, monoverticillate; stipe 3.0–4.0 µm wide. Phialides ampulliform, 10–14 per vesicle, 9–11 × 2.5–3.5 µm. Conidia in long irregular columns, broadly ellipsoidal, smooth to finely roughened, 3.0–4.0 µm.

Penicillium clavistipitatum Visagie, Houbraken & K. Jacobs, **sp. nov.** MycoBank MB809961. Fig. 24.

Etymology: Referring to the vesiculate stipe apices of the species.

Diagnosis: *Penicillium clavistipitatum* grows restrictedly on CYA and MEA and has rough walled stipes that end in vesicles up to 10 µm diam.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium fuscum*-clade.

Typus: **South Africa**, Malmesbury, Riverlands, Fynbos, soil, isolated by C.M. Visagie (holotype CBS H-21882, culture ex-type CBS 138650 = DTO 182-E5 = CV 336 = KAS 4112 = DAOM 241092).

Barcode and molecular based ID: ITS barcode: KM189667 (alternative markers: *BenA* = KM088912; *CaM* = KM089299; *RPB2* = KM089686).

Description: Colony diam, 7 d, in mm: CYA 17–23; CYA15°C 11–13; CYA30°C no growth to 15 mm; CYA37°C no growth; MEA 20–25; YES 18–27; DG18 18–20; CYAS 6–9; ratio CYAS:CYA 0.35–0.4; CREA 7–10, weak growth, no acid production.

Sporulation on CYA dense; conidia greenish grey to dark green, colony texture velutinous, low, plane; mycelium white; exudate absent; soluble pigment not produced; margin subsurface, narrow, entire; reverse yellowish white to greyish green to olive grey. Sporulation on YES moderately dense; conidia dull green, colony texture velutinous, low, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish grey to light yellow to olive brown. Sporulation on DG18 absent to sparse; conidia greyish green, colony texture velutinous, low, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to olive. Sporulation on MEA dense; conidia greyish green to dark green, colony texture velutinous, low, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse light yellow to yellowish brown. Ehrlich reaction negative.

Sclerotia absent. Conidiophores monoverticillate; stipes rough walled, 20–120 × 2.5–3.5 µm, vesicles 5.5–10 µm diam. Phialides ampulliform, 22–35 per stipe, 7–9 × 2.5–3.5 µm. Conidia globose, distinctly rough walled, 2.5–3 × 2.5–3 µm.

Penicillium contaminatum Houbraken, **sp. nov.** MycoBank MB809962. Fig. 25.

Etymology: Named after the origin of the type strain, a culture contaminant.

Diagnosis: The species is phylogenetically closely related to *P. yezoense*, but differs by more restricted growth on DG18 (21–25 *vs* 30–39 mm) and CYAS (30–35 *vs* 37–47 mm), less sporulation on YES and CYAS and conidia that are broadly ellipsoidal compared to the ellipsoidal conidia of *P. yezoense*. The reverse of *P. contaminatum* on YES is in shades of yellow, while that of *P. yezoense* is often in brown shades.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium thomii*-clade.

Typus: **United Kingdom**, Kew, Surrey, culture contaminant (holotype CBS H-21866, culture ex-type CBS 345.52 = DTO 091-A3 = IMI 049057).

Barcode and molecular based ID: ITS barcode: KM189554 (alternative markers: *BenA* = KM088793; *CaM* = KM089178; *RPB2* = KM089565).

Description: Colony diam, 7 d, in mm: CYA 42–55; CYA15°C 16–22; CYA30°C 28–38; CYA37°C no growth; MEA 46–50; YES 51–57; DG18 21–25; CYAS 30–35; ratio CYAS:CYA 0.61–0.73; CREA 11–17, weak growth and no acid production.

Weak sporulation on CYA; colony texture velvety, radially sulcate, deep; conidia grey green; mycelium white; exudate absent or present in the centre as small clear droplets; soluble absent or brown (CBS 346.59); margin entire to slightly irregular; reverse cream or brown. Sporulation on YES absent or poor, conidia dull grey green; mycelium white; soluble pigments absent; reverse yellow. Moderate sporulation on DG18, conidia dull green; reverse (bright) yellow. Weak sporulation on MEA, colony texture velvety to slightly floccose; conidia dull green; exudate absent; reverse with yellow centre, colour medium under margins unaffected. Ehrlich reaction yellow.

Sclerotia absent. Conidiophores 150–250 µm long, apices vesiculate 4–7 µm diam, roughened, monoverticillate; stipe 2.5–3.5 µm wide. Phialides ampulliform with short narrow neck, 10–14(–16) per stipe, 8.5–11.5 × 2.5–3.5 µm. Conidia in long irregular columns, broadly ellipsoidal, smooth when young, finely roughened in older parts of the colony.

Penicillium flavisclerotiatum Visagie, Houbraken & K. Jacobs, **sp. nov.** MycoBank MB809963. Fig. 26.

Etymology: Referring to the yellow sclerotia produced by this species.

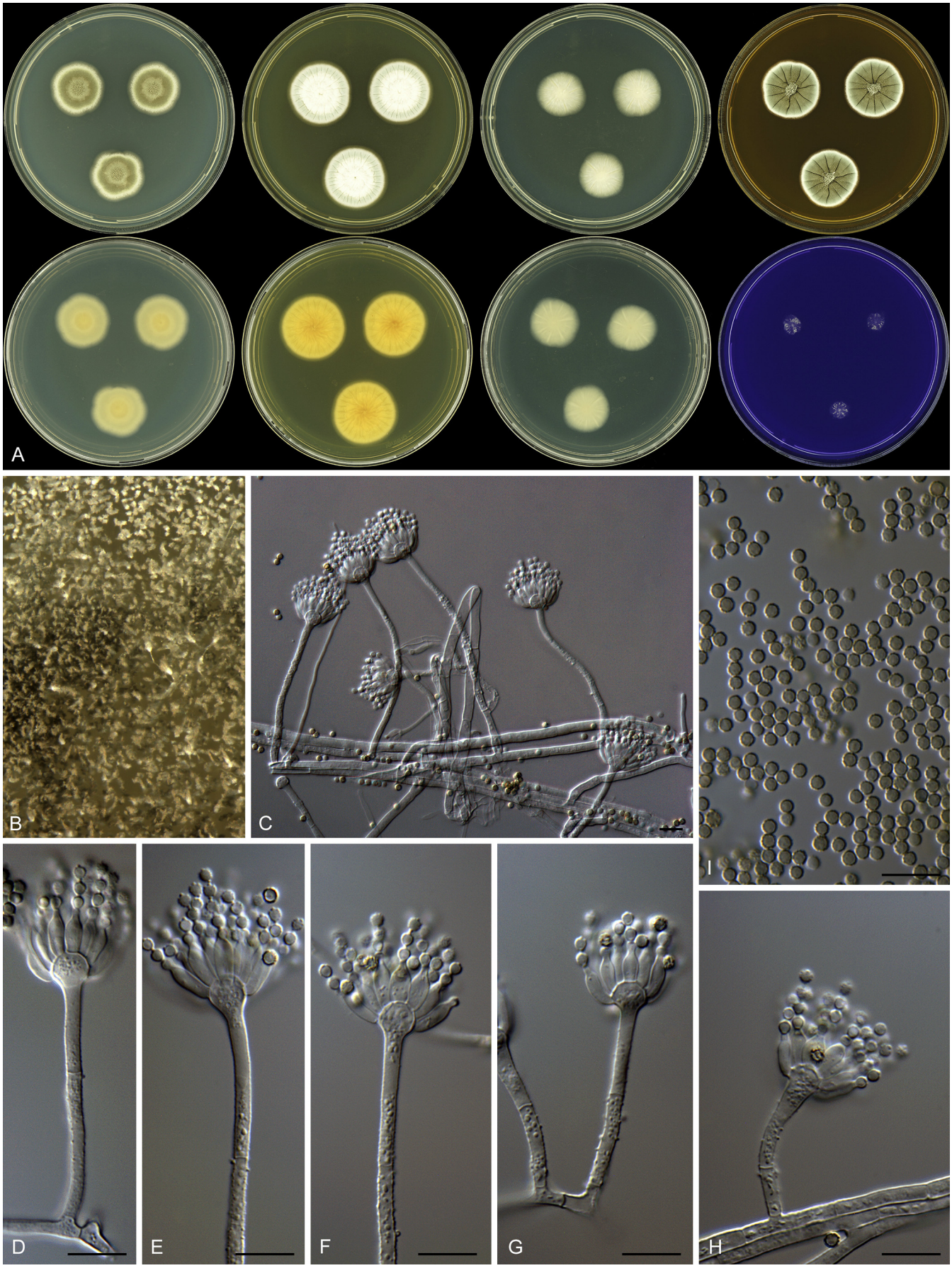

Fig. 24. *Penicillium clavistipitatum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Colony texture. C–H. Conidiophores. I. Conidia. Scale bars = 10 µm.

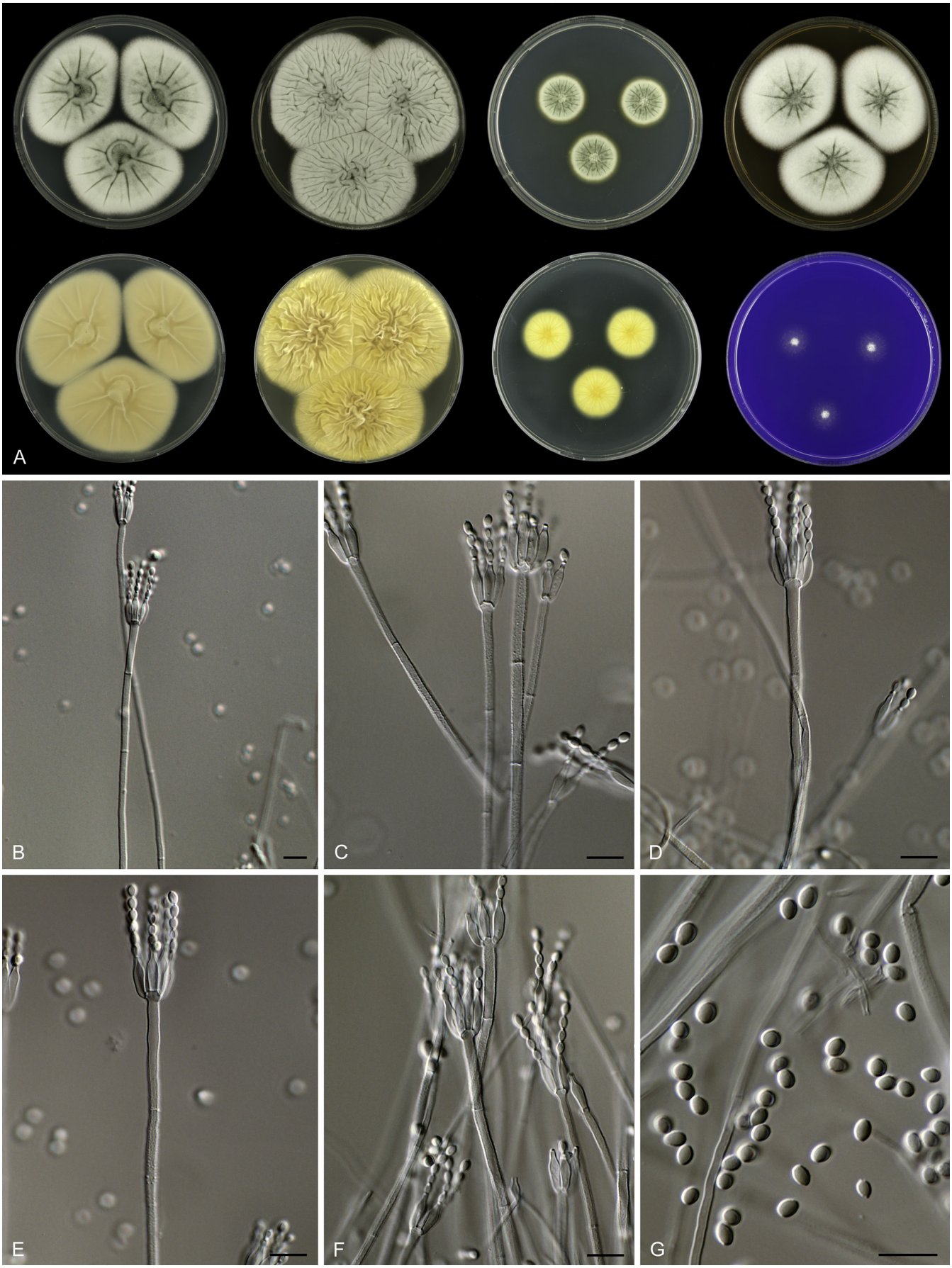

Fig. 25. *Penicillium contaminatum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

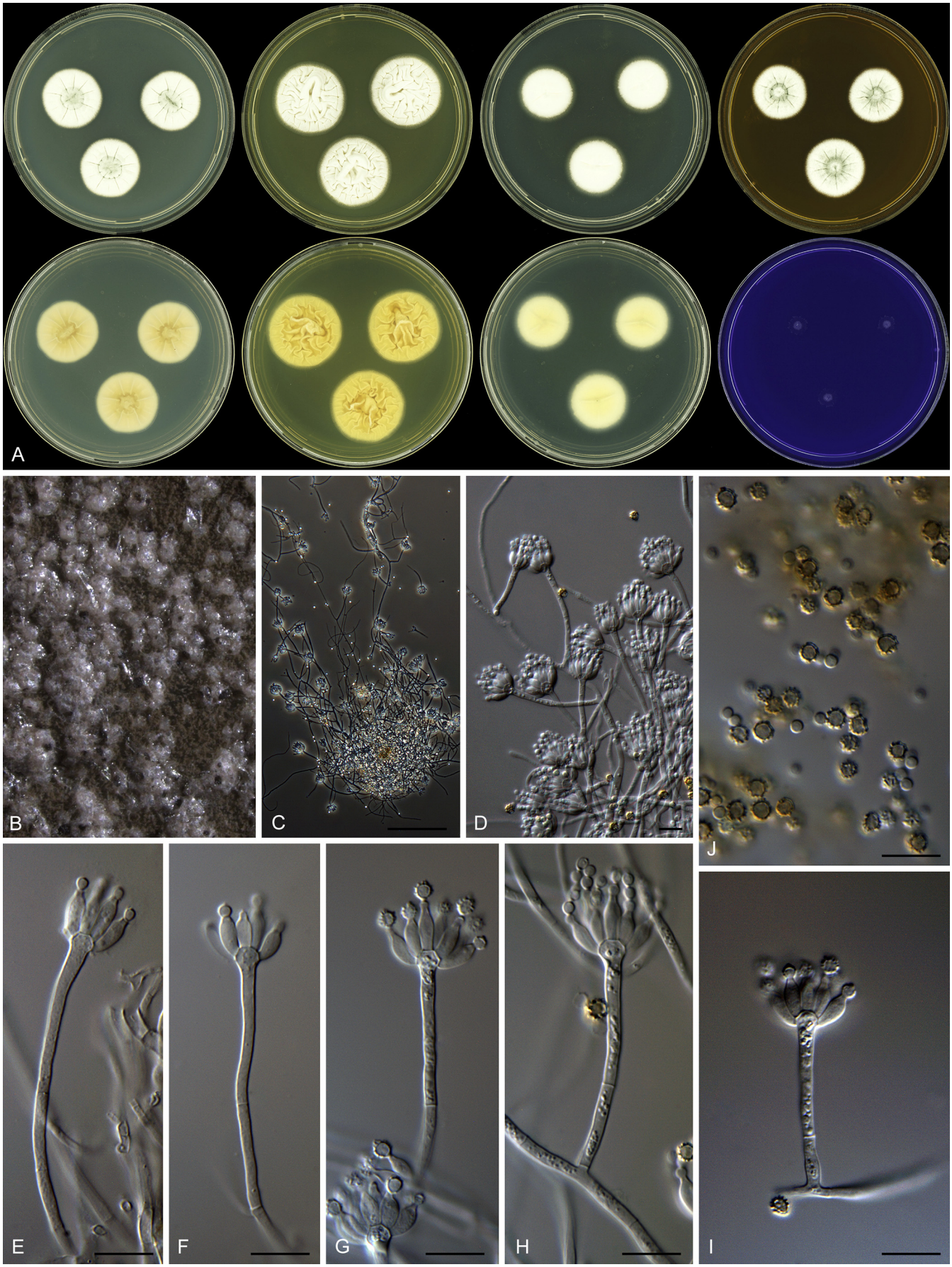

Fig. 26. *Penicillium flavisclerotiatum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Colony texture showing sclerotia. C–I. Conidiophores. J. Conidia. Scale bars = 10 µm.

Diagnosis: This species belongs to the *P. fuscum*-clade and is characterised by a slow growth rate on CYA, YES and MEA and the production of (pale) yellow sclerotia.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium fuscum*-clade.

Typus: **South Africa**, Western Cape, Stellenbosch mountain, Fynbos soil, isolated by C.M. Visagie (holotype CBS H-21879, culture ex-type CBS 137750 = DTO 180-I8 = CV 100 = DAOM 241157).

Barcode and molecular based ID: ITS barcode: KM189644 (alternative markers: *BenA* = KM088888; *CaM* = KM089275; *RPB2* = KM089662).

Description: Colony diam, 7 d, in mm: CYA 23–26; CYA15°C 10–18; CYA30°C 18–21; CYA37°C no growth; MEA 23–28; YES 30–35; DG18 25–27; CYAS 9–10; ratio CYAS:CYA 0.4; CREA 7–8, weak growth, acid not produced.

Sporulation on CYA moderately dense; conidia greyish green to dull green, colony texture velutinous and floccose, low, sulcate, cream to light yellow sclerotia produced; mycelium white; exudate clear; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to greyish orange. Sporulation on YES absent; conidia , colony texture floccose, moderately deep, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to light yellow. Sporulation on DG18 very sparse; conidia white to greenish white, colony texture floccose, low, lightly sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to light yellow. Sporulation on MEA moderately dense; conidia greyish green to dull green, colony texture floccose, low, sulcate, yellow sclerotia sometimes present; mycelium white; exudate absent to clear; soluble pigment not produced; margin low, narrow, entire; reverse brownish yellow to yellowish brown. Ehrlich reaction negative.

Sclerotia produced on CYA and MEA, 80–160 × 70–150 µm. Conidiophores monoverticillate; stipes smooth walled, 23–80 × 2–3.5 µm, vesicles 4–5.5 µm diam. Phialides ampulliform, 8–20 per stipe, 6–9 × 2.5–3.5 µm. Conidia heavy rough to spiny walls, some strains only finely rough walled, globose to somewhat subglobose, 2–3.5 × 2–3.5 µm.

Penicillium grevilleicola Houbraken & Quaedvlieg, **sp. nov.** MycoBank MB809964. Fig. 27.

Etymology: Referring to the host from which the type strain was isolated, *Grevillea ilicifolia*.

Diagnosis: The species has dark pure green conidia on MEA, whereas the phylogenetically related species *P. crocicola*, *P. austroafricanum*, *P. jejuense* have dull or dull grey-green conidia. Furthermore, *P. grevilleicola* has strongly floccose colonies and broadly ellipsoidal conidia.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium thomii*-clade.

Typus: **Australia**, Kangaroo Island, Kingscote, leaf of *Grevillea ilicifolia*, isolated by J. Houbraken & W. Quaedvlieg (holotype CBS H-21871, culture ex-type CBS 137775 = DTO 174-E6).

Barcode and molecular based ID: ITS barcode: KM189630 (alternative markers: *BenA* = KM088874; *CaM* = KM089261; *RPB2* = KM089648).

Description: Colony diam, 7 d, in mm: CYA 44–48; CYA15°C 26–30; CYA30°C 18–22; CYA37°C no growth; MEA 43–47; YES 48–52; DG18 26–30; CYAS 33–37; ratio CYAS:CYA 0.74–0.78; CREA 18–22, weak growth and no acid production.

Weak sporulation on CYA and only in the centre; colony texture floccose, radially sulcate, deep; mycelium white; exudate present in the centre as small clear droplets; soluble pigments absent; margin entire; reverse pale crème brown with. Sporulation on YES absent or very poor, mycelium white; soluble pigments absent; reverse orange-yellow. Strong sporulation on DG18, conidia dark green; reverse yellow. Moderate to good sporulation on MEA, colony texture floccose; conidia pure green; few exudate droplets, small, pale yellow; reverse with yellow centre, colour medium under margins unaffected; sclerotia present under mycelium and becoming visible after 14 d incubation. Ehrlich reaction negative.

Sclerotia present, orange-brown, 200–350 µm; hard; consisting of polygonal cells; no asci or ascospores observed. Conidiophores 200–400 µm long, stipes strongly vesiculate, 5–8 µm diam, roughened, monoverticillate; stipe 3.0–4.0 µm wide. Phialides ampulliform with short neck, densely packed, up to 18 per stipe, 10–12 × 3.0–3.5 µm. Conidia in long irregular columns, broadly ellipsoidal, smooth to finely roughened.

Penicillium hoeksii Houbraken, **sp. nov.** MycoBank MB809965. Fig. 28.

Etymology: Named after Toon Hoeks, who assisted during the collection of the soil sample from which the type strain was isolated.

Diagnosis: The species is characterised by the production of brown soluble pigments on CYA, OA and/or CYAS, smooth walled stipes, finely roughened (broadly) ellipsoidal conidia and no growth on CYA at 30 °C. This species grows better on CYA at 25 °C than at 15 °C, in contrast to *P. zhuangii*.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium hoeksii*-clade.

Typus: **Belgium**, Postel, soil under Compact Rush (*Juncus conglomeratus*), isolated by J. Houbraken (holotype CBS H-21860, culture ex-type CBS 137776 = DTO 192-H4).

Barcode and molecular based ID: ITS barcode: KM189707 (alternative markers: *BenA* = KM088954; *CaM* = KM089341; *RPB2* = KM089728).

Description: Colony diam, 7 d, in mm: CYA 20–28; CYA15°C 12–18; CYA30°C no growth; CYA37°C no growth; MEA 20–28; YES 26–33; DG18 18–26; CYAS 13–20; ratio CYAS:CYA 0.60–0.67(–0.85); CREA 2–7, weak growth and no acid production.

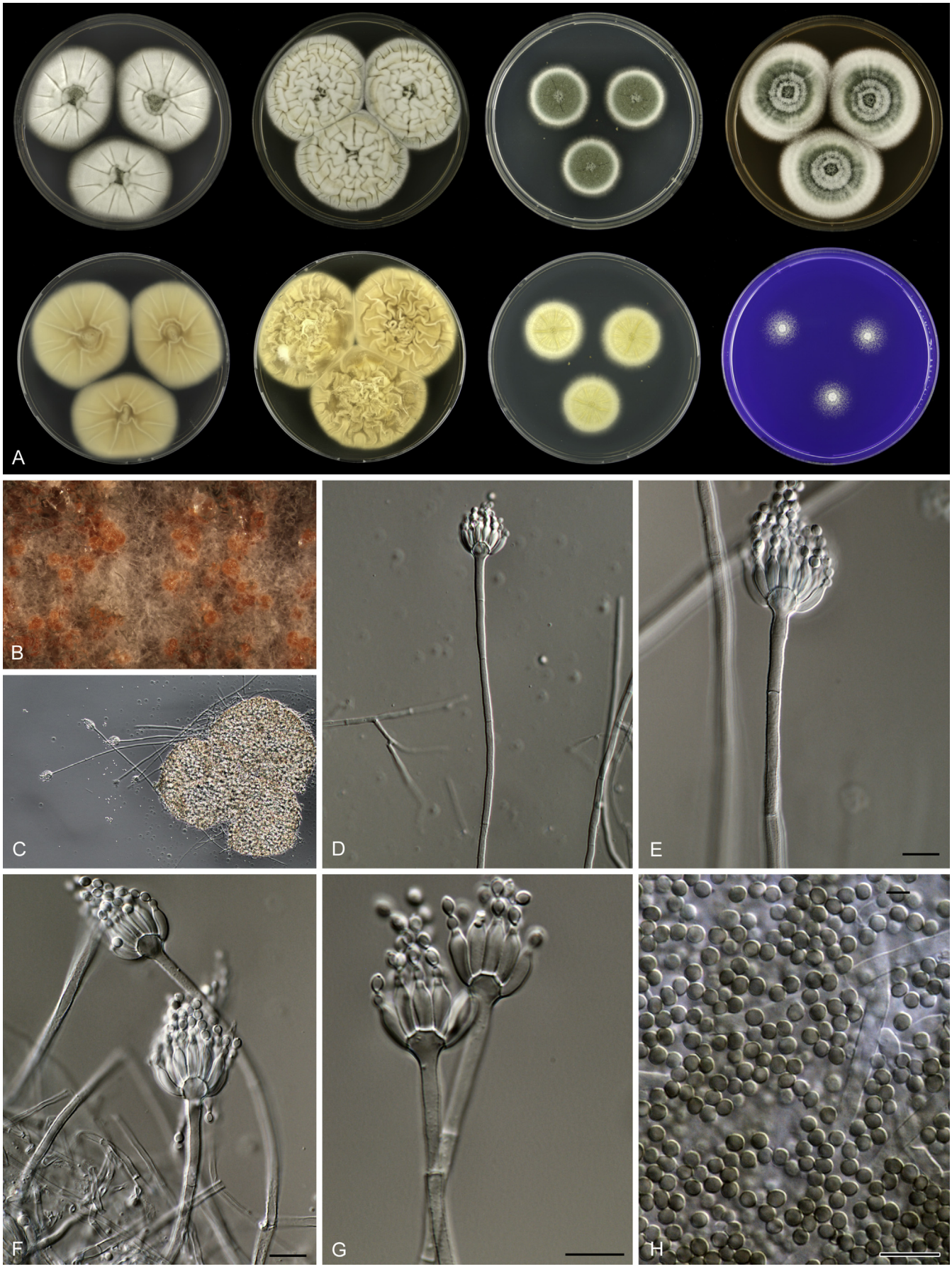

Fig. 27. *Penicillium grevilleicola*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B, C. Sclerotia. D–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

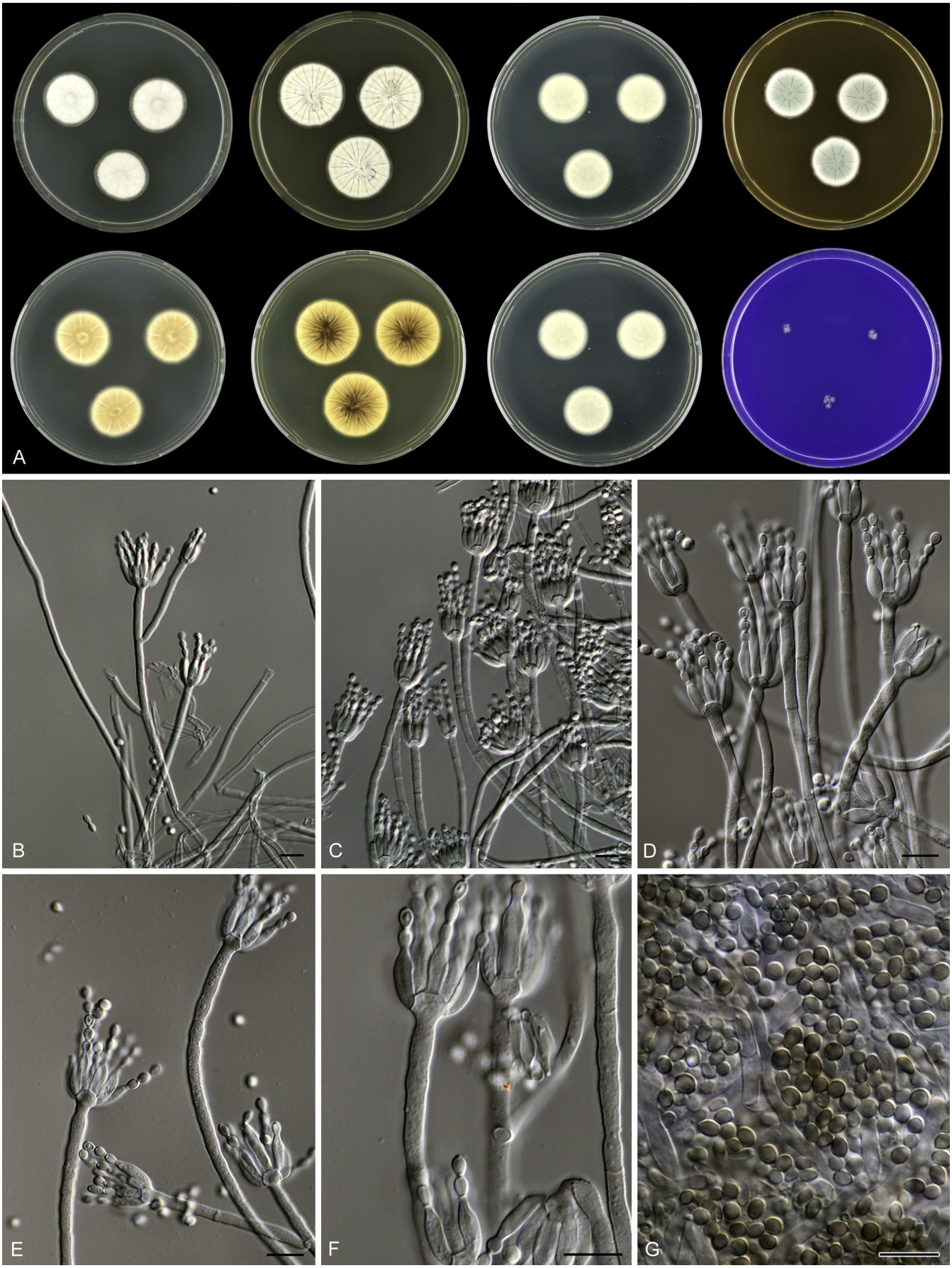

Fig. 28. *Penicillium hoeksii*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Sporulation on CYA absent or weak; colony texture velvety, radially sulcate, deep; conidia grey green; mycelium white; exudate absent or present in the centre as small clear or yellow droplets; soluble pigment production strong, brown; margin entire; reverse in shades of brown, sometimes with dark brown centre. Sporulation on YES absent or poor, conidia grey green; mycelium white or pale crème; soluble pigment production weak, brown; reverse brown with dark brown centre. Good sporulation on DG18, colony texture floccose to slightly funiculose; conidia dull green; reverse transparent, pale brown or brown. Moderate sporulation on MEA, colony texture velvety, sometimes with slightly floccose centre; conidia greyish blue green; exudate absent; reverse in shades of brown. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 50–250 µm long, stipes slightly vesiculate up to 5.0 µm diam, smooth walled, monoverticillate, in older parts divaricate with metulae in intercalary positions, intergrading with monoverticillate conidiophores; stipe 3.0–3.5 µm wide. Phialides ampulliform, (1–)2–5(–8) per stipe, 9.0–11.5 × 2.5–3.5 µm. Conidia in short distorted chains, (broadly) ellipsoidal, finely roughened, 3.0–3.7 × 2.5–3.0 µm.

Penicillium infra-aurantiacum Visagie, Houbraken & K. Jacobs, **sp. nov.** MycoBank MB809966. Fig. 29.

Etymology: Referring to the orange reverse pigmentation that is diagnostic for the species.

Diagnosis: This species is phylogenetically related to *P. sublectaticum* and *P. malmesburiense*. *Penicillium infra-aurantiacum* differs from *P. sublectaticum* having irregularly shaped colonies on CYA, while those of *P. malmesburiense* are polygonal in outline.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium sublectaticum*-clade.

Typus: **South Africa**, Western Cape, Malmesbury, Riverlands, bracts of *Protea repens* infructescence, isolated by C.M. Visagie (holotype CBS H-21880, culture ex-type CBS 137747 = DTO 183-C3 = CV 1518 = DAOM 241145).

Barcode and molecular based ID: ITS barcode: KM189684 (alternative markers: *BenA* = KM088930; *CaM* = KM089317; *RPB2* = KM089704).

Description: Colony diam, 7 d, in mm: CYA 30–34; CYA15°C 21–23; CYA30°C 12–15; CYA37°C no growth; MEA 30–33; YES 33–35; DG18 25–30; CYAS 18–21; ratio CYAS:CYA 0.6; CREA 15–16, weak growth, no acid production.

Sporulation on CYA moderately dense; conidia greyish turquoise, colony texture velutinous and floccose, low, sulcate; margin slightly polygonal; mycelium white; exudate clear to orange; soluble pigment yellow, inconspicuous; margin low, narrow, polygonal in face view; reverse yellowish white to brownish orange to yellowish brown to brown. Sporulation on YES moderately dense; conidia greyish green, colony texture velutinous and floccose, moderately deep, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to yellowish grey to olive to greyish orange. Sporulation on DG18 dense; conidia dark green, colony texture velutinous and floccose, low, slightly sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to greyish green to light yellow to orange. Sporulation on MEA moderately dense; conidia greyish green, colony texture velutinous and floccose, low, sulcate; mycelium white; exudate clear; soluble pigment not produced; margin low, narrow, entire; reverse light yellow to yellowish brown to brown. Ehrlich reaction negative.

Conidiophores monoverticillate; stipes smooth walled, 100–230 × 2–3 µm, vesicles 4.5–6 µm diam. Phialides ampulliform, 10–18 per stipe, 8.5–11 × 2.5–3 µm. Conidia rough walled, globose, 2.5–3.5 µm.

Penicillium kiamaense Houbraken & Pitt, **sp. nov.** MycoBank MB809967. Fig. 30.

Etymology: Named after Kiama, the location of the type strain of this species.

Diagnosis: This species is phylogenetically unique and most closely related to species of the *P. glabrum*- and *P. thomii*-clades. Phenotypically is most closely related to *P. subspinulosum*, but can be differentiated by the production of dark (dull) green conidia on OA and MEA and a reverse on YES in shades of orange.

In: subgenus *Aspergilloides*, section *Aspergilloides*, undefined clade (basal to *P. glabrum* and *P. thomii*-clade).

Typus: **Australia**, NSW, Barren Grounds Nature Reserve, near Kiama, soil, isolated by J.I. Pitt (holotype CBS H-21857, culture ex-type CBS 137947 = FRR 6087 = DTO 056-I6).

Barcode and molecular based ID: ITS barcode: KM189506 (alternative markers: *BenA* = KM088743; *CaM* = KM089128; *RPB2* = KM089515).

Description: Colony diam, 7 d, in mm: CYA 33–37; CYA15°C 22–26; CYA30°C 12–16; CYA37°C no growth; MEA 33–37; YES 37–41; DG18 23–27; CYAS 24–28; ratio CYAS:CYA 0.73–0.75; CREA 18–22, weak growth and no acid production.

Sporulation on CYA weak, only in the centre; colony texture velvety, radially sulcate, deep; conidia dull grey-green; mycelium white; exudate present in the centre as small pale yellow droplets; soluble pigment production weak, yellow-brown; colony in face view polygonal; reverse yellowish brown in the centre, brown at the margins. Sporulation on YES poor; mycelium white to pale cream; soluble pigment production strong, orange-brown; reverse orange with an orange-brown centre. Good sporulation on DG18, colony texture crustose; conidia dull green; reverse yellow. Good sporulation on MEA, colony texture velvety; conidia dark green; exudate present, pale; reverse with yellow centre, colour medium under margins unaffected. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 50–250 µm long, stipes vesiculate up to 6.0 µm diam, finely rough walled, predominantly monoverticillate, sometimes with a short branch up to 14 µm long, stipe 3.0–4.0 µm wide. Phialides ampulliform, 5–12 per stipe, 9.0–11.0 × 2.5–3.5 µm. Conidia in moderately long chains, globose to subglobose, distinctly ornamented with striations, 3.0–3.5 µm.

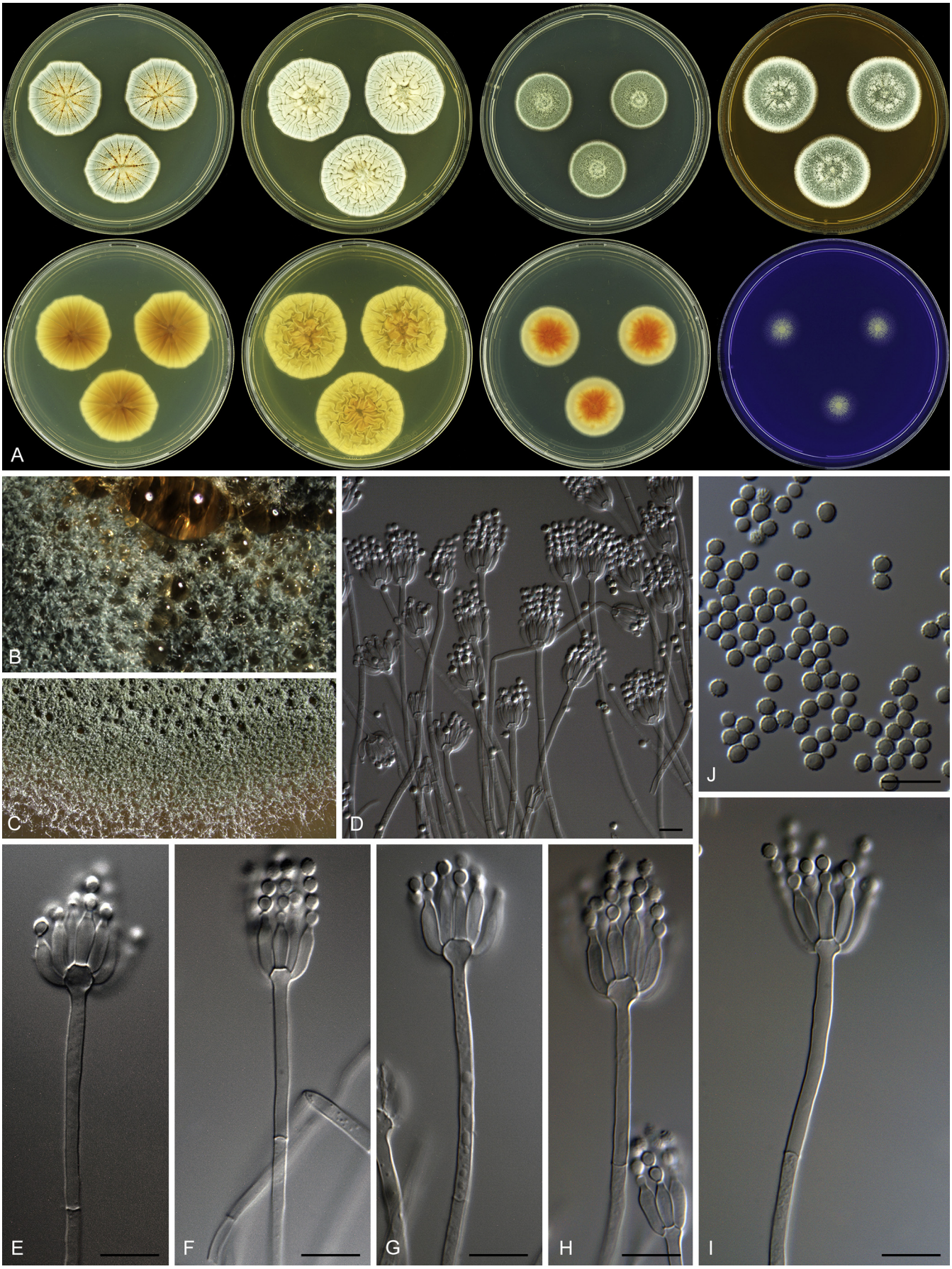

Fig. 29. *Penicillium infra-aurantiacum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B, C. Sclerotia. D–I. Conidiophores. J. Conidia. Scale bars = 10 µm.

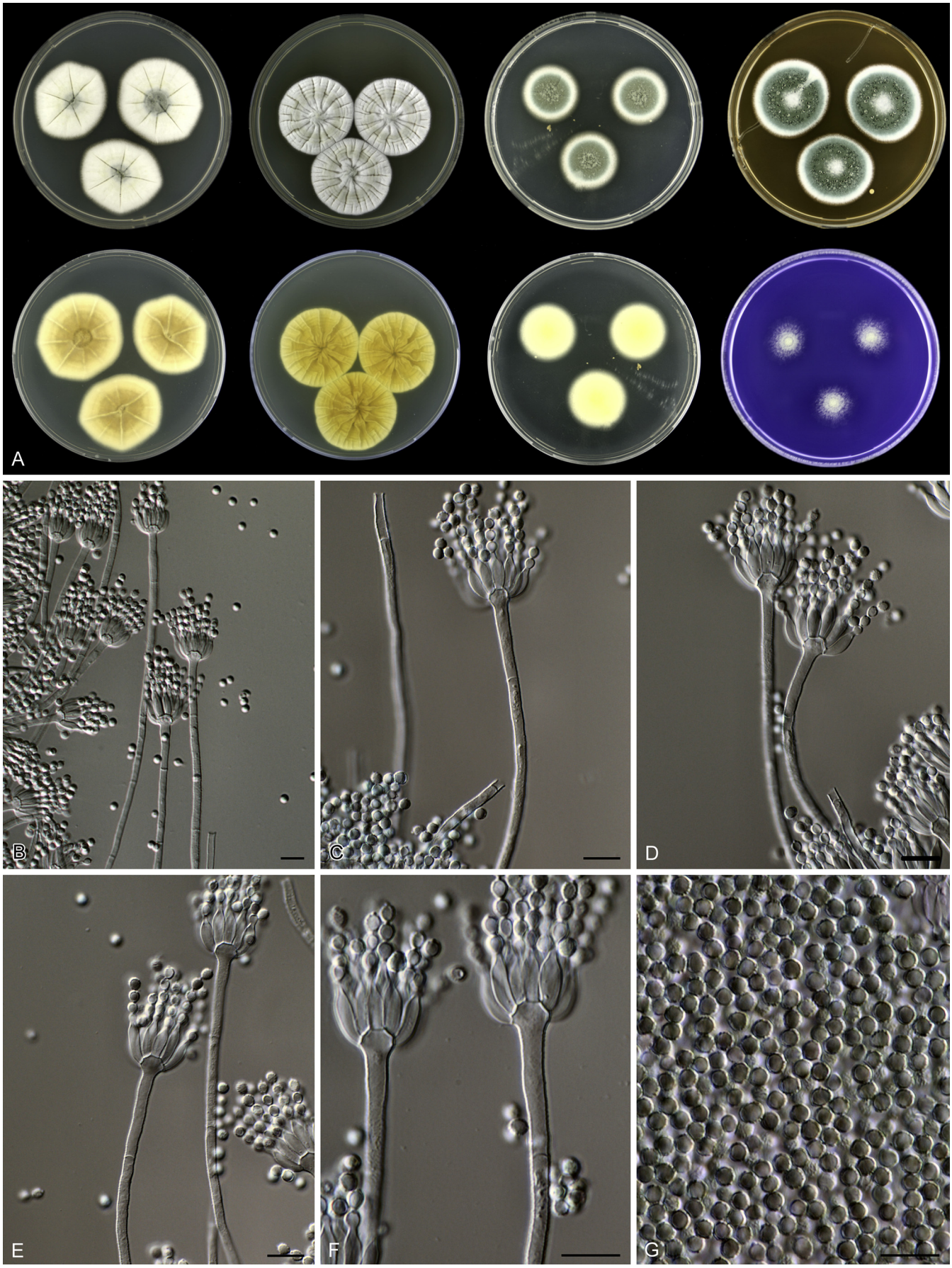

Fig. 30. *Penicillium kiamaense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Penicillium longicatenatum Visagie, Busby, Houbraken & K. Jacobs, **sp. nov.** MycoBank MB809968. Fig. 31.

Etymology: Referring to the long chains of conidia produced by this species in culture.

Diagnosis: This species is phylogenetically unique and in common with other species of the *P. thomii*-clade, it produces sclerotia on CYA and MEA and grows well on CYA at 30 °C. Conidia are subglobose.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium vagum*-clade.

Typus: **South Africa**, Western Cape, Malmesbury, Riverlands, Fynbos, soil, isolated by C.M. Visagie (holotype CBS H-21875, culture ex-type CBS 137735 = DTO 180-D9 = CV 2847 = DAOM 241119).

Barcode and molecular based ID: ITS barcode: KM189636 (alternative markers: *BenA* = KM088880; *CaM* = KM089267; *RPB2* = KM089654).

Description: Colony diam, 7 d, in mm: CYA 40–45; CYA15°C 23–27; CYA30°C 25–35; CYA37°C no growth; MEA 35–45; YES 45–50; DG18 30–35; CYAS 35–45; ratio CYAS:CYA 0.9–1; CREA 15–20, weak growth, acid not produced.

Sporulation on CYA moderately dense; conidia greyish green to dull green to greyish green, colony texture velutinous and floccose, low, sulcate, cream to light brown sclerotia produced; mycelium white; exudate clear to yellow; soluble pigment yellow to yellowish brown; margin low, narrow, entire; reverse greyish yellow near margin, elsewhere brown. Sporulation on YES moderately dense; conidia greyish green to dull green, colony texture velutinous, low to moderately deep, sulcate; mycelium white; exudate absent; soluble pigment yellow; margin low, narrow, entire; reverse light yellow to greyish yellow. Sporulation on DG18 moderately dense to dense; conidia greyish green to dull green to greyish green, colony texture velutinous, low, slightly sulcate; mycelium white; exudate absent; soluble pigment yellow; margin low, narrow, entire; reverse light yellow to greyish green. Sporulation on MEA moderately dense; conidia greyish green to dull green to greyish green, colony texture velutinous and floccose, low to moderately deep, sulcate, cream to greyish brown sclerotia present; mycelium white; exudate clear to yellow; soluble pigments not produced; margin low, narrow to wide, entire; reverse greyish orange to brownish yellow to yellowish brown. Ehrlich reaction negative.

Sclerotia produced on CYA and MEA, 50–250 × 40–250 µm. Conidiophores monoverticillate; stipes smooth walled, 60–330 × 2.5–3.5 µm, vesicles 4–9 µm diam. Phialides ampulliform, 12–25 per stipe, 7–11 × 2.5–4 µm. Conidia finely rough walled, subglobose, 2.5–3.5 × 2–3 µm.

Penicillium malmesburiense Visagie, Houbraken & K. Jacobs, **sp. nov.** MycoBank MB809969. Fig. 32.

Etymology: Referring to the collection site of the type strain, Malmesbury.

Diagnosis: The species is phylogenetically closely related to *P. infra-aurantiacum* and *P. sublectaticum*, but differs by its pale reverse on CYA, CYAS and DG18.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium sublectaticum*-clade.

Typus: **South Africa**, Western Cape, Malmesbury, Riverlands, mite from *Protea repens* infructescence, isolated by C.M. Visagie (holotype CBS H-21872, culture ex-type CBS 137744 = DTO 182-H5 = CV 1180 = DAOM 241144).

Barcode and molecular based ID: ITS barcode: KM189676 (alternative markers: *BenA* = KM088921; *CaM* = KM089308; *RPB2* = KM089695).

Description: Colony diam, 7 d, in mm: CYA 34–35; CYA15°C 20–23; CYA30°C 20–22; CYA37°C no growth; MEA 30–33; YES 34–35; DG18 24–26; CYAS 24–28; ratio CYAS:CYA 0.7–0.8; CREA 15–20, weak growth, acid not produced.

Sporulation on CYA moderately dense; conidia dull green to greyish green, colony texture velutinous, low, sulcate; mycelium white; exudate clear; soluble pigment not produced; margin low, narrow, entire; reverse greenish grey to greyish yellow, with dark olive spots at centre. Sporulation on YES moderately dense; conidia dull green to dark green, colony texture velutinous, moderately deep, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to olive. Sporulation on DG18 moderately dense; conidia dull green to dark green, colony texture velutinous with some floccose areas, low, slightly sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse greenish grey to greyish yellow, with dark olive spots at centre. Sporulation on MEA moderately dense to dense; conidia greyish green to dark green, colony texture velutinous, low, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish brown to brown. Ehrlich reaction negative.

Conidiophores monoverticillate; stipes smooth walled, 35–115 × 2–3 µm, vesicles 4–6.5 µm diam. Phialides ampulliform, 10–20 per stipe, 8.5–10 × 3–3.5 µm. Conidia finely rough walled, subglobose, 2.5–3.5 × 2.5–3 µm.

Penicillium pulvis Houbraken, Visagie, Samson & Seifert, **sp. nov.** MycoBank MB809970. Fig. 33.

Etymology: Referring to dust, the substrate from which the type strain was isolated.

Diagnosis: This species grows more restrictedly on CYA than other species of the *P. glabrum*-clade. It has a (dark) brown reverse on CYA, YES and DG18 and produces brown soluble pigment on CYA.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium glabrum*-clade.

Typus: **South Africa**, Kuils River, house dust, collected by K. Jacobs, isolated by E. Whitfield & K. Mwange (holotype CBS H-21878, culture ex-type CBS 138432 = DTO 180-B7).

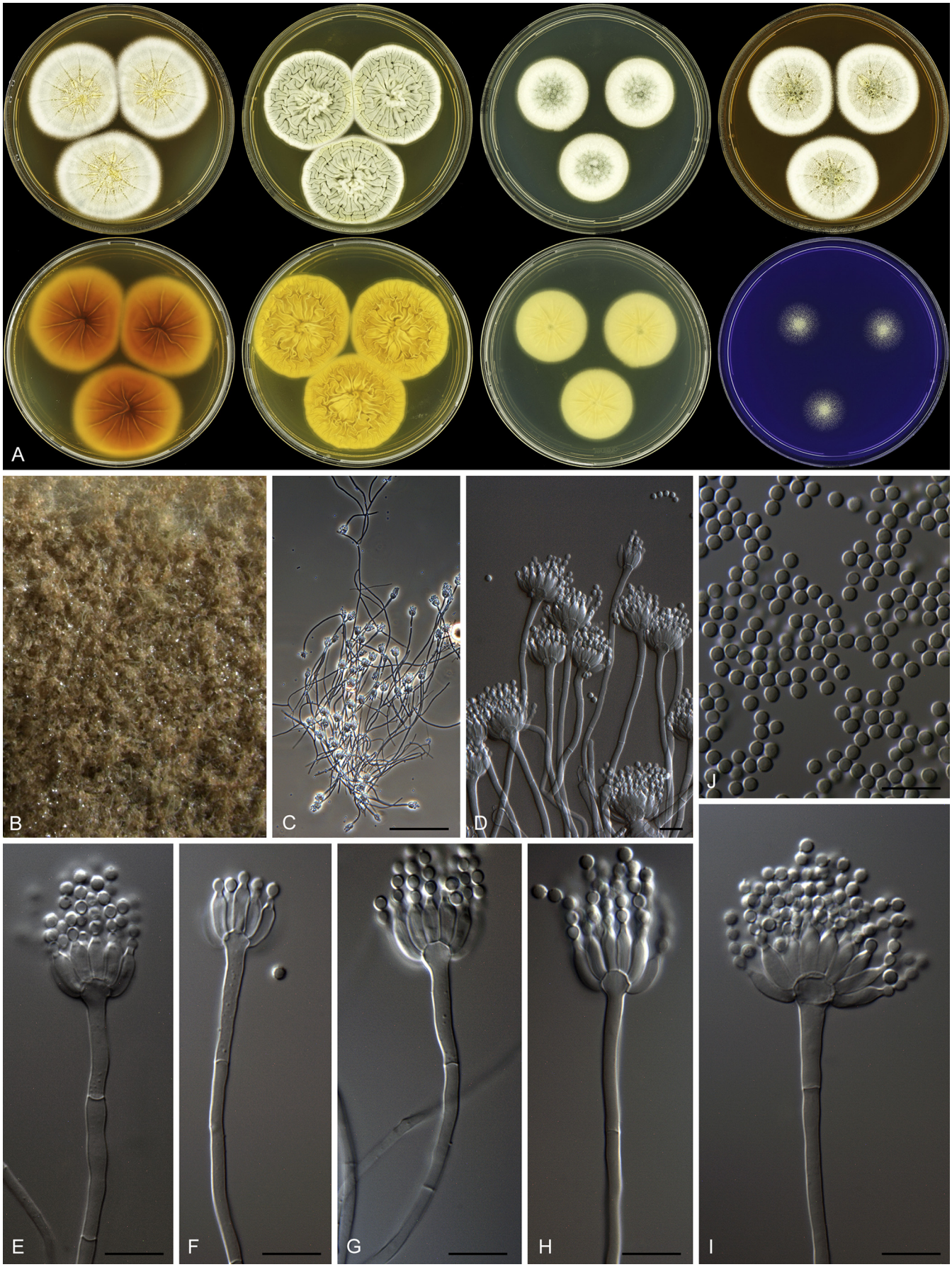

Fig. 31. *Penicillium longicatenatum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Colony texture. C–I. Conidiophores. J. Conidia. Scale bars = 10 µm.

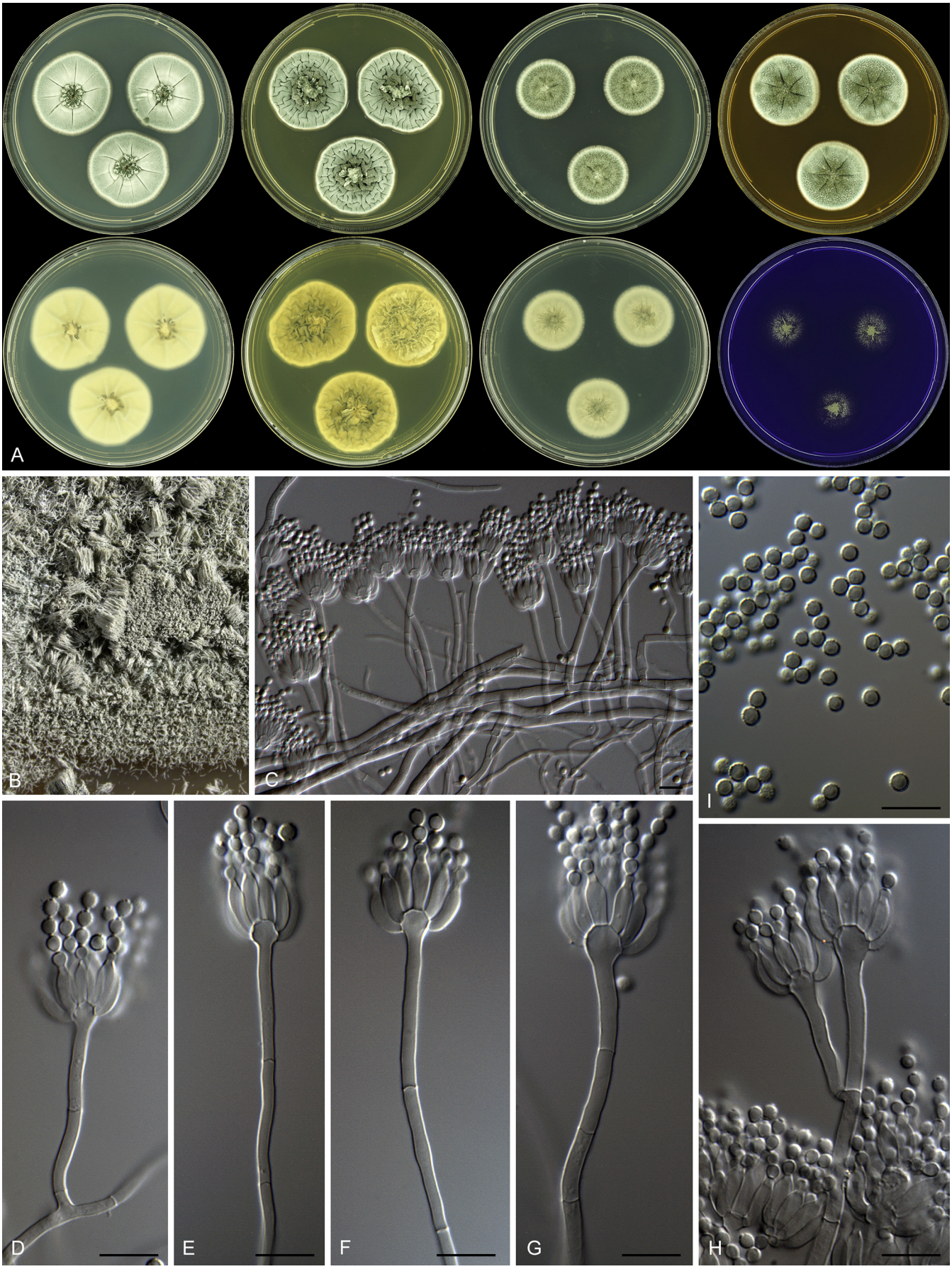

Fig. 32. *Penicillium malmesburiense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Colony texture. C–H. Conidiophores. I. Conidia. Scale bars = 10 µm.

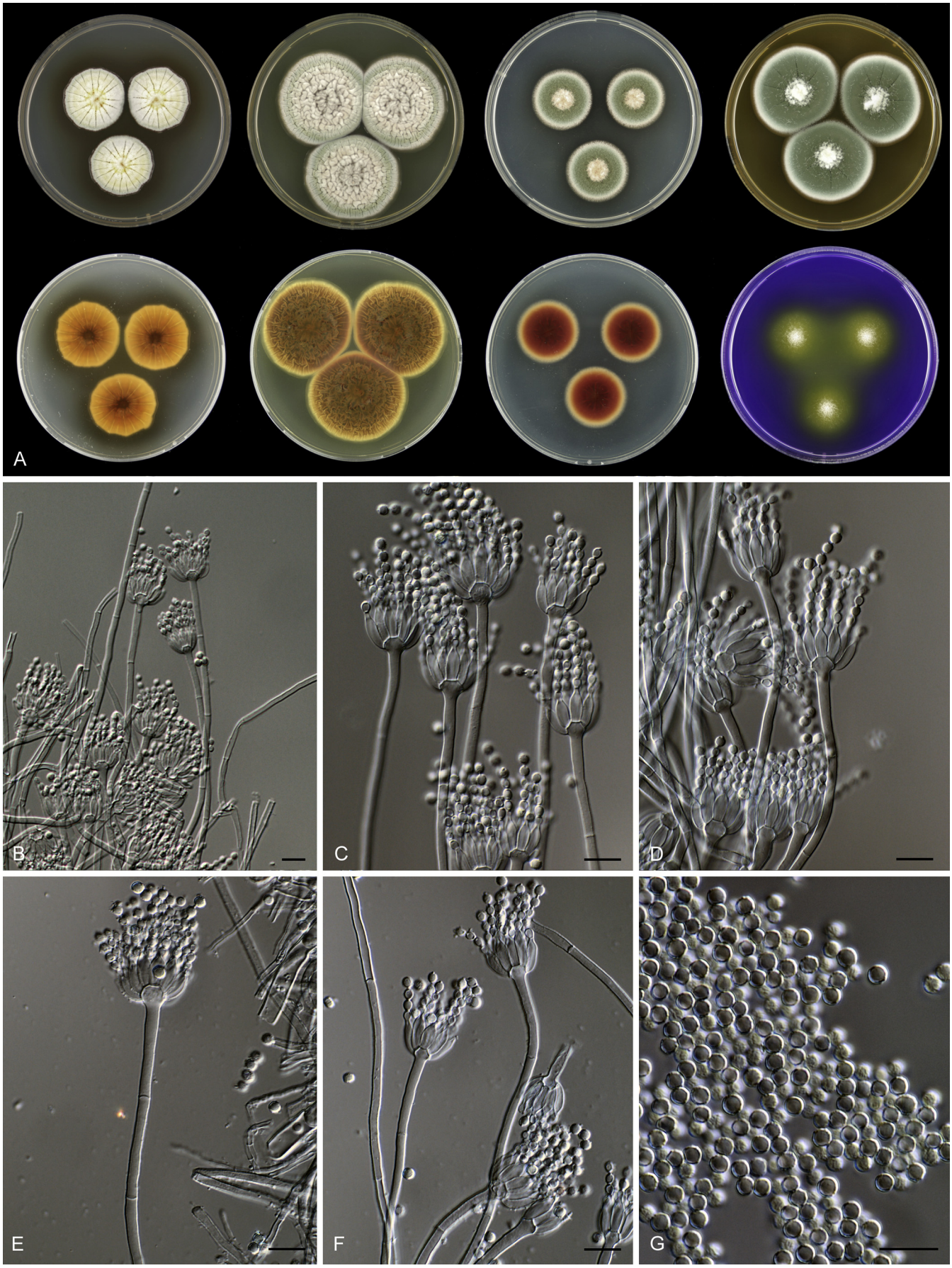

Fig. 33. *Penicillium pulvis*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Barcode and molecular based ID: ITS barcode: KM189632 (alternative markers: *BenA* = KM088876; *CaM* = KM089263; *RPB2* = KM089650).

Description: Colony diam, 7 d, in mm: CYA 26–32; CYA15°C 22–28; CYA30°C 24–30; CYA37°C no growth; MEA 37–43; YES 39–45; DG18 23–29; CYAS 21–27; ratio CYAS:CYA 0.75–0.90; CREA 19–25, weak growth and moderate acid production.

Sporulation on CYA weak; radially sulcate, deep; mycelium pale beige; exudate present as small orange-yellow droplets; soluble pigment production strong, brown; margin irregular; reverse brown, with dark brown centre. Sporulation on YES absent weak, mycelium white; conidia grey green; soluble pigment not produced; reverse dark brown. Moderate to good sporulation on DG18; colony texture velvety to slightly floccose; conidia dull green; reverse dark brown. Good sporulation on MEA, colony texture velvety; conidia dull green; exudate absent; reverse dark brown in the centre, reverse colour not affecting medium. Ehrlich reaction negative.

Sclerotia absent. Conidiophores, 100–300 µm long, apices vesiculate up to 6.5 µm wide, smooth to finely walled, strictly monoverticillate, stipe 2.5–3.5 µm wide. Phialides ampulliform, 4–16 per stipe, 9.0–10.0 × 2.5–3.0 µm. Conidia in long well-defined chains, globose to subglobose, finely ornamented, 2.7–3.2 µm.

Penicillium ranomafanaense Houbraken & Hagen, **sp. nov.** MycoBank MB809971. Fig. 34.

Etymology: Named after Ranoma fana, the location of the type specimen.

Diagnosis: The species is phylogenetically related to *P. verhagenii*, but differs in having an orange reverse on DG18 and smooth to finely roughened stipes.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium verhagenii*-clade.

Typus: **Madagascar**, Ranoma fana, soil, isolated by F. Hagen & J. Houbraken (holotype CBS H-21862, culture ex-type CBS 137953 = DTO 085-A5).

Barcode and molecular based ID: ITS barcode: KM189541 (alternative markers: *BenA* = KM088779; *CaM* = KM089164; *RPB2* = KM089551).

Description: Colony diam, 7 d, in mm: CYA 26–33; CYA15°C 20–26; CYA30°C no growth; CYA37°C no growth; MEA 25–33; YES 33–43; DG18 22–30; CYAS 12–27; ratio CYAS:CYA 0.50–0.85; CREA 5–10, weak growth and no acid production.

Sporulation on CYA weak to moderate; colony texture velvety, radially sulcate, deep; conidia dull green becoming dark green in the centre; mycelium white; exudate absent; soluble pigment production strong, yellow to orange; margin entire or slightly polygonal in face view; reverse yellow-orange with orange-red centre. Sporulation on YES absent; mycelium pale crème; soluble pigment not produced; reverse orange. Good sporulation on DG18, colony texture slightly floccose; conidia dull to dark green; mycelium white, reverse orange. Good sporulation on MEA, colony texture velvety; conidia dark green in the centre, towards dull green at the edge, always with a blue element; exudate absent; reverse not affecting the medium. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 100–250 µm long, with smooth or finely roughened stipes; irregularly branched, predominantly symmetrically biverticillate, older conidiophores becoming divaricate due to having secondary growth of the stipe by proliferation at the apex, stipe 2.5–3.5 µm wide. Metulae in terminal whorl of 3–6, of unequal length, (9.0–)11.0–16.5(–22) × 2.5–3.5 µm. Phialides, two types present, predominantly ampulliform, short, 8.5–9.5 × 2.5–3.5 µm, also larger phialides present, cylindrical, (9–)10.5 × 14(–16) µm, (2–)4–10(–14) per metulae. Conidia in short distorted chains, roughened, occasionally with striations, variable in shape: subglobose to broadly ellipsoidal in DTO 085-A5, 2.5–3.0 µm in size, (broadly) ellipsoidal in DTO 085-A8 2.5–3.0 × 2.0–2.7 µm.

Penicillium rudallense Houbraken, Visagie & Pitt, **sp. nov.** MycoBank MB809972. Fig. 35.

Etymology: Referring to the location of the type strain, Rudall River National Park.

Diagnosis: This species belongs phylogenetically to the *P. glabrum*-clade and can be differentiated by the production of distinctly ornamented, dark green conidia on CYA and MEA, and good growth on CYA.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium glabrum*-clade.

Typus: **Australia**, WA, Rudall River National Park, soil, isolated by A.D. Hocking (holotype CBS H-21867, culture ex-type CBS 138162 = FRR 6085 = DTO 056-I4).

Barcode and molecular based ID: ITS barcode: KM088741 (alternative markers: *BenA* = KM089126; *CaM* = KM189504; *RPB2* = KM089513).

Description: Colony diam, 7 d, in mm: CYA 35–46; CYA15°C 22–28; CYA30°C 25–37; CYA37°C 0–7; MEA 39–46; YES 48–54; DG18 35–43; CYAS 35–40; ratio CYAS:CYA 0.80–0.92; CREA 18–32, poor growth and moderate acid production.

Sporulation on CYA good; radially sulcate, deep; colony texture velvety; conidia dark green; mycelium white; exudate absent or present as yellow droplets; soluble pigment absent or light brown; margin slightly polygonal; reverse (pale) orange-brown or brown with dark brown centre. Sporulation on YES strong; conidia dark dull green, mycelium beige; soluble pigments absent; reverse yellow, orange-yellow or crème with brown centre. Good sporulation on DG18, colony texture granular or floccose; conidia dull green; reverse pale or orange. Good sporulation on MEA, colony texture velvety, sometimes slightly floccose; conidia dark green; exudate absent. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 150–400 µm long, stipes slightly vesiculate in young parts of the colony, inflated in older parts, up to 6.0 µm, smooth or finely rough walled, predominantly

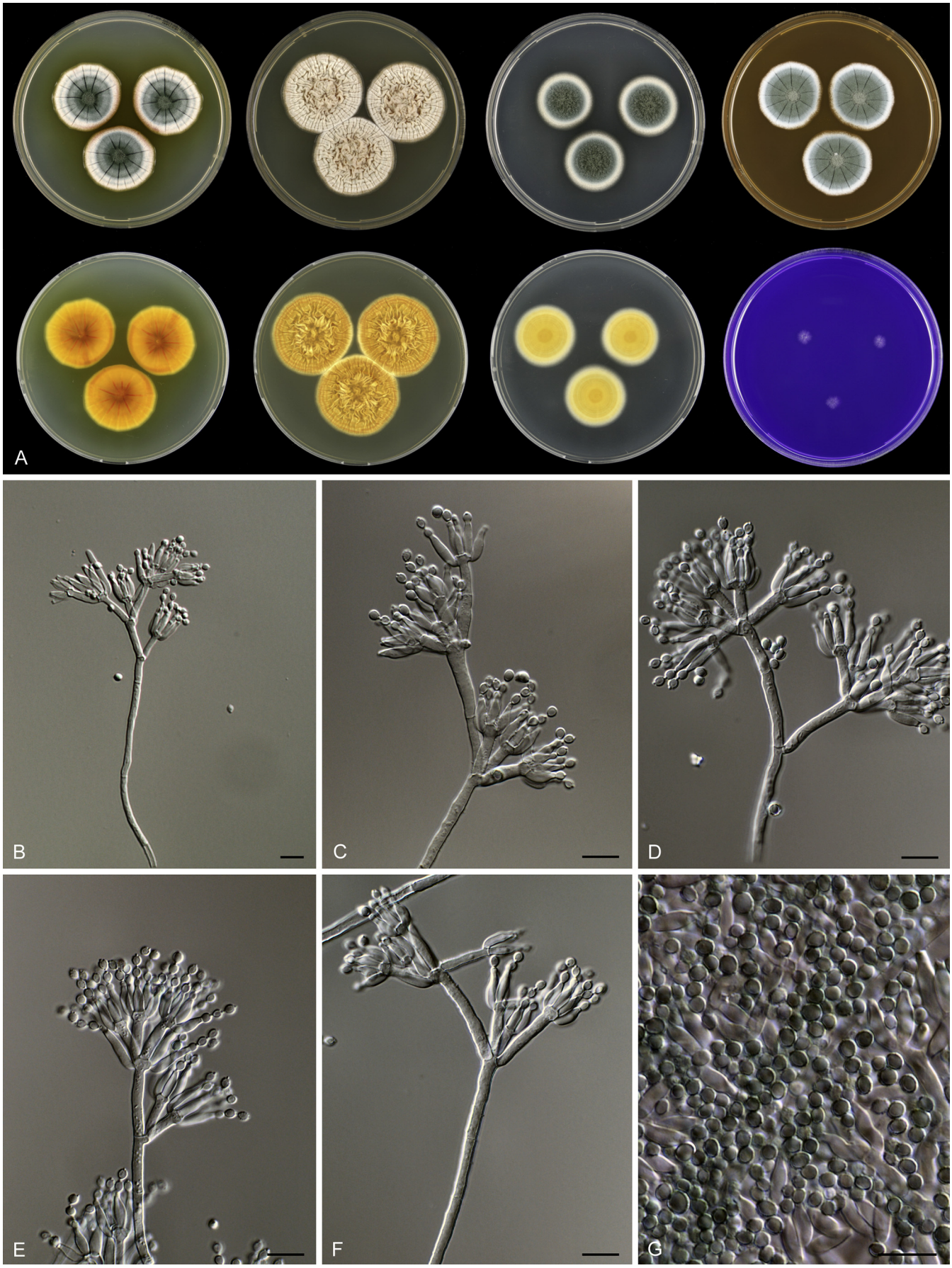

Fig. 34. *Penicillium ranomafanaense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

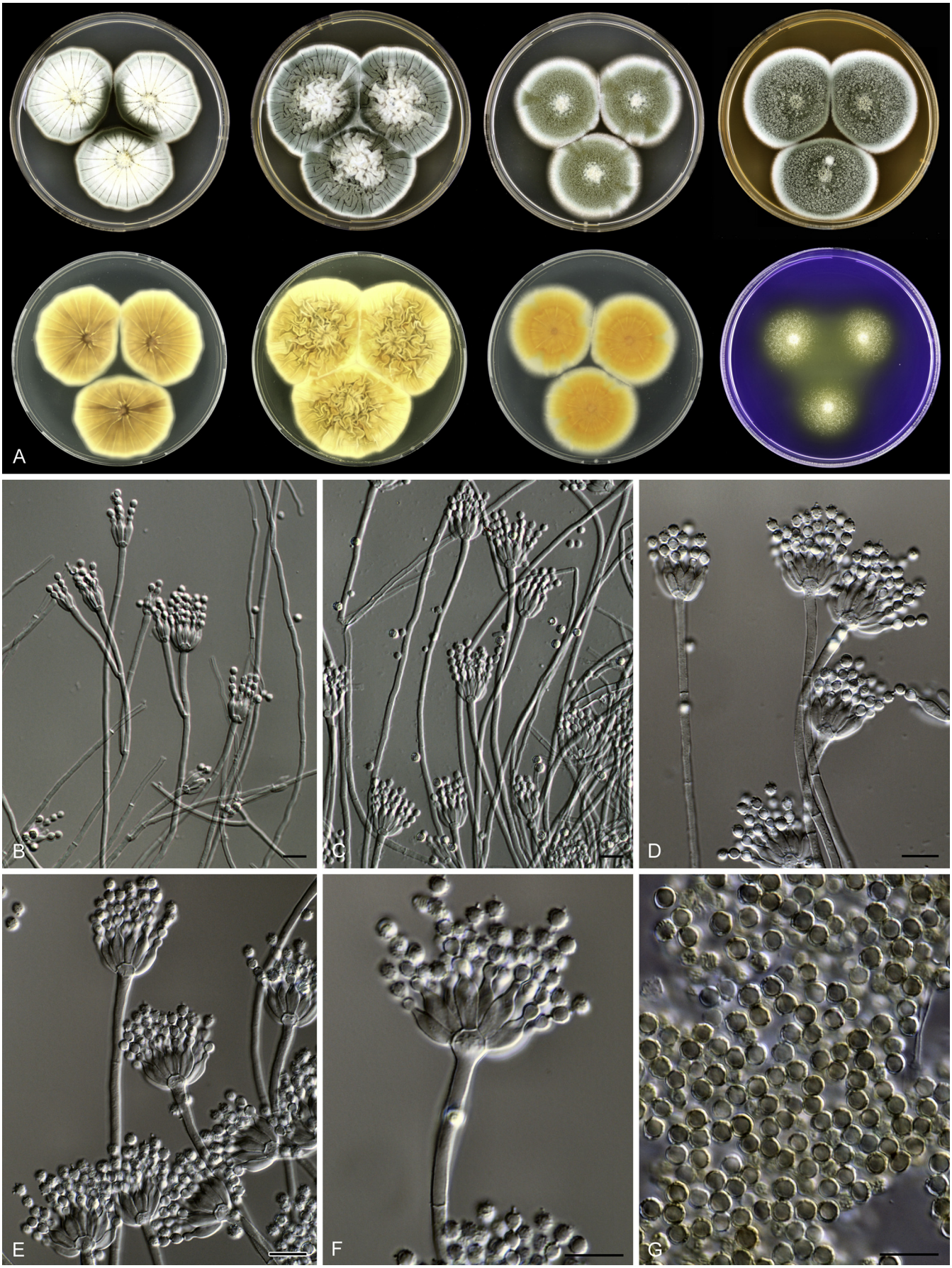

Fig. 35. *Penicillium rudallense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

monoverticillate, sometimes symmetrically biverticillate or with additional branch, stipe 2.0–3.0 µm wide. Phialides ampulliform with short neck, 6–14 per stipe, 8.0–10.0 × 2.5–3.5 µm. Conidia in long well-defined chains, globose, distinctly ornamented, slightly striated and inner and outer cell wall visible, 3.0–3.5 µm.

Penicillium sterculiniicola Houbraken, **sp. nov.** MycoBank MB809973. Fig. 36.

Etymology: Named after compost (*sterculinium*), the substrate from which the type was isolated.

Diagnosis: This species grows well on CREA, colonies at CYA at 30 °C after 7 d (29–) are 37–47 mm diam, and no sporulation occurs on CYA and YES. Stipes are rough walled and the conidia 2.7–3.7 µm diam.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium spinulosum*-clade.

Typus: **USA**, spawn run compost (holotype CBS H-21877, culture ex-type CBS 122426 = DTO 031-A4).

Barcode and molecular based ID: ITS barcode: KM189464 (alternative markers: *BenA* = KM088693; *CaM* = KM089078; *RPB2* = KM089465).

Description: Colony diam, 7 d, in mm: CYA (25–)39–45; CYA15°C 17–22; CYA30°C (29–)37–47; CYA37°C no growth; MEA 37–55; YES 35–45; DG18 22–35; CYAS 20–28; ratio CYAS:CYA 0.55–0.63(–0.84); CREA 24–34, good growth and weak to moderate acid production, followed by a delayed base production.

Sporulation on CYA absent or very weak; radially sulcate, deep; mycelium white; exudate absent; soluble pigment not produced; margin entire, irregular in DTO 216-I4; reverse in shades of brown, pale brown, crème or brown. Sporulation on YES absent, mycelium white; soluble pigment not produced; reverse yellow-brown. Good sporulation on DG18, colony texture crustose; conidia dull green; reverse pale or transparent. Good sporulation on MEA, colony texture floccose, occasionally velvety to floccose; conidia dark green or dark dull green; exudate present as large droplets, clear or pale brown. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 50–250 µm long, apices vesiculate in older parts of the colony, less pronounced in younger parts, up to 6.5 µm diam, stipe finely roughened to distinct rough walled, predominantly monoverticillate, sometimes with divergent additional branch up to 15 µm long, stipe 2.5–3.5 µm wide. Phialides ampulliform, 6–14 per stipe, 9.0–11.0 × 2.5–3.5 µm. Conidia in long distorted chains, globose, distinctly ornamented with striations, 2.5–4.0 µm.

Penicillium sublectaticum Houbraken, Frisvad, Samson & Seifert, **sp. nov.** MycoBank MB809974. Fig. 37.

Etymology: Referring to “under the bed”, the location from where the type strain was isolated from.

Diagnosis: The species is phylogenetically closely related to *P. infra-aurantiacum* and *P. malmesburiense*. Phenotypically, it is most similar to *P. infra-aurantiacum* and differs by irregular margins on CYA and a dark brown reverse on CYA with (yellow) brown margins.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *P. sublectaticum*-clade.

Typus: **New Zealand**, Dunedin, house dust, collected by T. Atkinson, 2009, isolated by E. Whitfield and K. Mwange (holotype CBS H-21955, culture ex-type: CBS 138217 = DTO 244-G2).

Barcode and molecular based ID: ITS barcode: KM189761 (alternative markers: *BenA* = KM089010; *CaM* = KM089397; *RPB2* = KM089784).

Description: Colony diam, 7 d, in mm: CYA 25–35; CYA15°C 17–25; CYA30°C 5–15; CYA37°C no growth; MEA 27–35; YES 30–37; DG18 23–30; CYAS 18–25; ratio CYAS:CYA 0.67–0.73; CREA 8–17, weak growth and no acid production.

Moderate sporulation on CYA and only in the centre; colony texture velvety; conidia grey green; radially sulcate, deep; mycelium white; exudate present as red-brown droplets; soluble pigments present, poor, red-brown; margin irregular; reverse brown or dark brown centre with (yellow-)brown edge. Sporulation on YES absent, mycelium white; soluble pigments absent; reverse reddish brown. Good sporulation on DG18; colony texture floccose; conidia dull green; reverse red-brown. Moderate sporulation on MEA, colony texture floccose; conidia dark dull green; few exudate droplets, small, pale yellow or clear; reverse brown. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 40–250 µm long, stipes predominantly non-vesiculate, occasionally slightly vesiculate in older parts of the colony, up to 4.0 µm, smooth walled, predominantly monoverticillate, occasionally with additional monoverticillate branch; stipe 2.5–3.5 µm wide. Phialides ampulliform to cylindrical, (2–)4–12 per stipe, 8–10 × 2.0–3.0 µm. Conidia in moderate to long well-defined columns, globose to subglobose, distinctly ornamented with striations, 3.0–3.5 µm.

Penicillium subspinulosum Houbraken, **sp. nov.** MycoBank MB809975. Fig. 38.

Etymology: Referring to the close relationship with *P. spinulosum*.

Diagnosis: The species is phylogenetically close to *P. spinulosum* and related species, but differs by its poor on CREA, velvety colonies on CYA and restricted growth on CYA30°C (4–18(–22) mm).

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium spinulosum*-clade.

Typus: **Poland**, soil, isolated by J. Houbraken & B. Byskal (holotype CBS H-21856, culture ex-type CBS 137946 = DTO 041-F2).

Barcode and molecular based ID: ITS barcode: KM189483 (alternative markers: *BenA* = KM088719; *CaM* = KM089104; *RPB2* = KM089491).

Description: Colony diam, 7 d, in mm: CYA (24–)36–41; CYA15°C 18–30; CYA30°C 4–18(–22); CYA37°C no growth; MEA (28–)35–42; YES 35–45; DG18 22–35; CYAS 25–35;

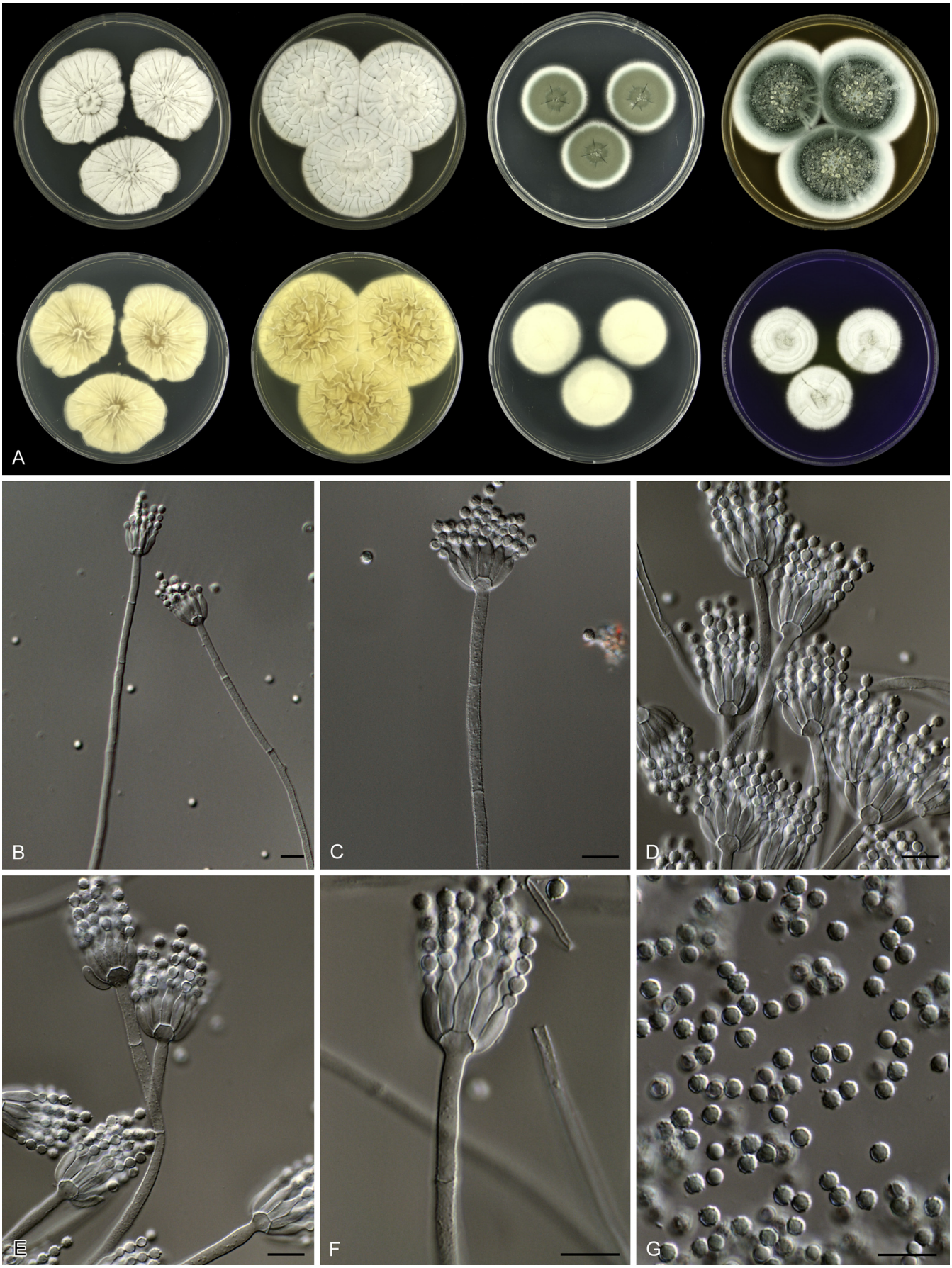

Fig. 36. *Penicillium sterculiniicola*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

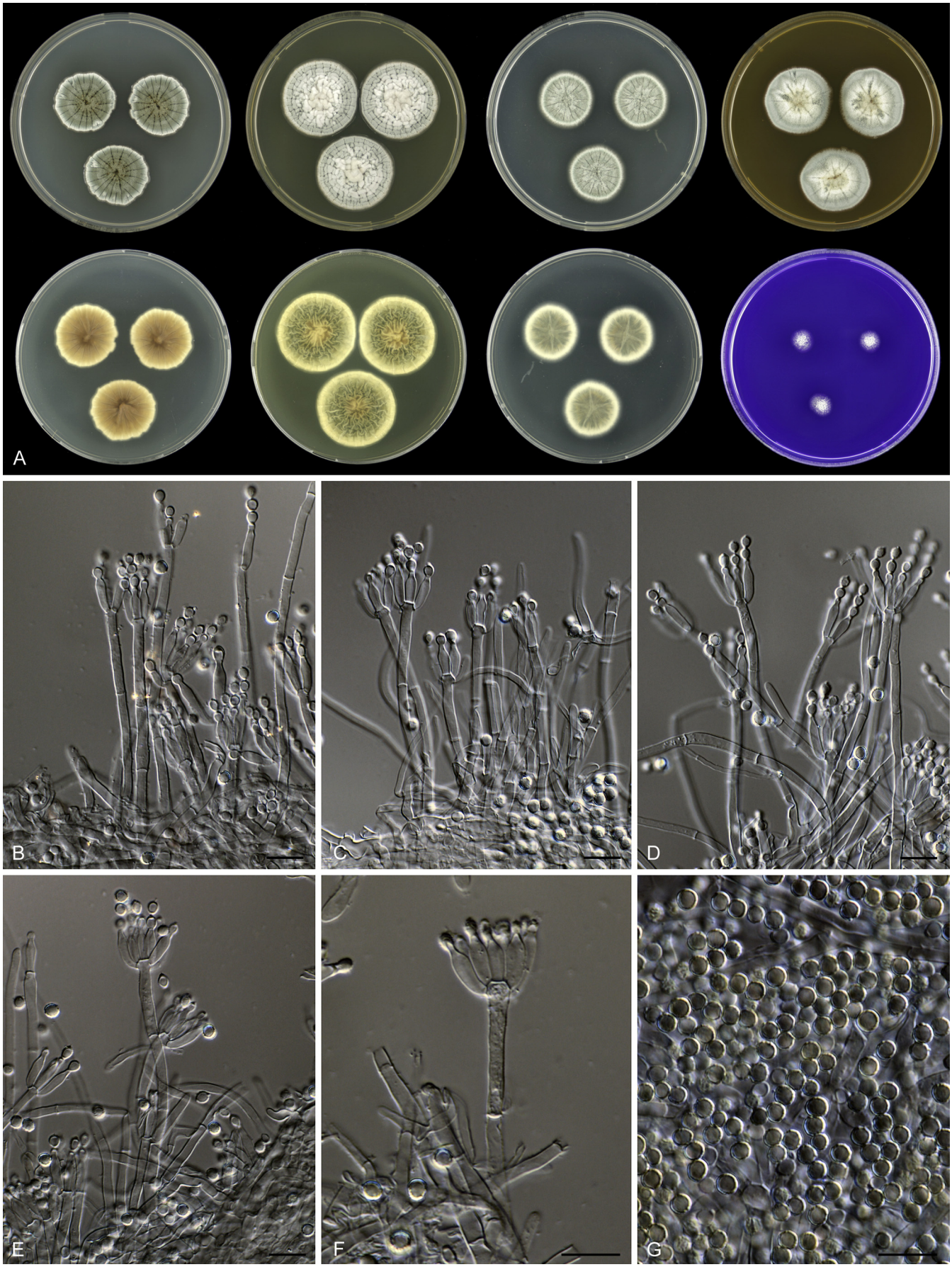

Fig. 37. *Penicillium sublectaticum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

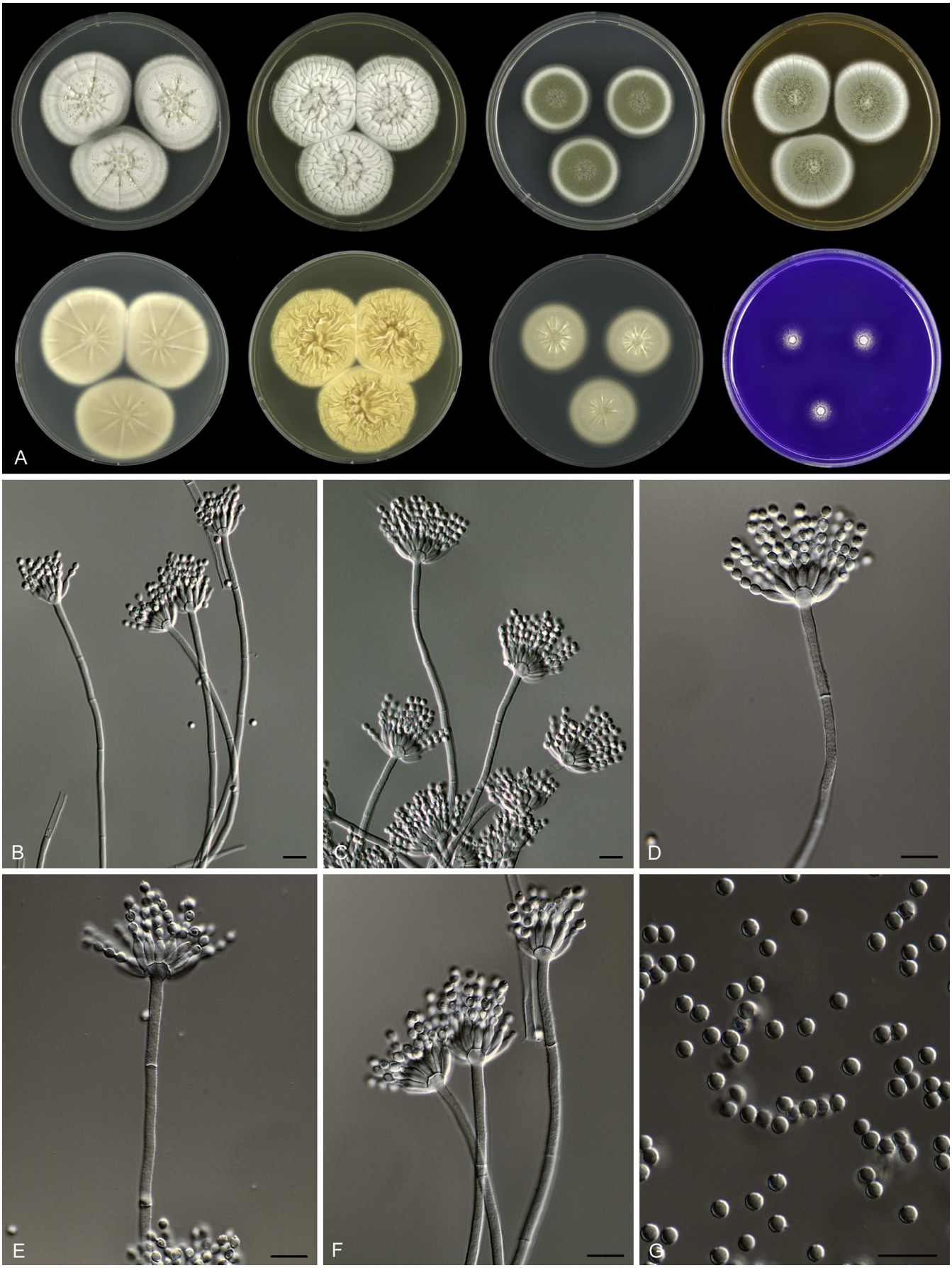

Fig. 38. *Penicillium subspinulosum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

ratio CYAS:CYA 0.65–0.90; CREA 10–18, poor growth and no acid production.

Sporulation on CYA poor; colony texture velvety, radially sulcate, deep; conidia pure green or dull green; mycelium white; exudate present, clear or pale yellow; soluble pigment absent except in DTO 297-D5 and then pale yellow; margin entire, occasionally lobate; reverse generally in shades of pale brown or cream (pale yellow). Sporulation on YES absent or poor, conidia pale dull green; mycelium white; soluble pigment not produced; reverse cream or pale brown. Good sporulation on DG18, colony texture velvety; conidia dull green; mycelium inconspicuous. Good sporulation on MEA, colony texture floccose in the centre, velvety at the edge; conidia pure green or pure to dull green; exudate if present as clear or pale yellow droplets; reverse brown or not affecting the medium. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 200–400 µm long, with finely roughened stipes, apices vesiculate up to 7 µm diam, predominantly monoverticillate, occasionally with additional branch up to 20 µm long, stipe 2.5–3.5 µm wide. Phialides ampulliform, densely packed, 6–16 per stipe, 7.5–9.5 × 2.0–3.0 µm. Conidia in moderately long, distorted chains, roughened, sometimes with striation or bars, globose, 2.5–3.3 µm.

Penicillium tsitsikammaense Houbraken, **sp. nov.** MycoBank MB809976. Fig. 39.

Etymology: Named after the collection site of the type strain, Tsitsikamma forest, South Africa.

Diagnosis: The species belongs to the *P. fuscum*-clade and can be distinguished from the other species by the absence of or poor growth on CYAS (0–2 mm), slow growth rate on CYA and YES, with sporulation absent or poor on all media.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium fuscum*-clade.

Typus: **South Africa**, Cape Province, Tsitsikamma Forest near Knysna, forest soil, isolated by D.B. Scott (holotype CBS H-21881, culture ex-type CBS 328.71 = DTO 006-I3 = CSIR 1092).

Barcode and molecular based ID: ITS barcode: KM189451 (alternative markers: *BenA* = KM088675; *CaM* = KM089060; *RPB2* = KM089447).

Description: Colony diam, 7 d, in mm: CYA 10–15; CYA15°C 8–12; CYA30°C 5–10; CYA37°C no growth; MEA 19–23; YES 20–25; DG18 17–21; CYAS 0–2; ratio CYAS:CYA 0.15–0.2; CREA 3–5, weak growth and no acid production.

Sporulation on CYA absent; mycelium pale pink or pinkish-beige; exudate absent; soluble pigment not produced; margin lobate (irregular); reverse pale yellow in colony centre, pale beige at the margin. Sporulation on YES absent, mycelium white; soluble pigment not produced; reverse pale yellow. Poor sporulation on DG18; colony texture velvety to floccose; conidia pale green; mycelium white; reverse pale green in the centre, pale at the margins. Sporulation on MEA absent; mycelium white; conidia produced after prolonged incubation, brown-green; sclerotia visible on the edge of the colony periphery, white; exudate absent; reverse centre pale orange and pale yellow at edge; Ehrlich reaction negative.

Sclerotia present on MEA, white, soft, consisting of polygonal cells, (30–)50–120 µm. Conidiophores monoverticillate, short, 25–50 µm long, smooth walled; non-vesiculate. Phialides ampulliform, often with a conspicuous neck, 2–4 per stipe, 8.5–10.0(–13) × 2.5–3.5 µm. Conidia in short distorted chains, globose to subglobose, thick walled, distinctly roughened, a proportion smooth walled, 2.5–3.5 µm diam, a minor proportion larger, up to 5.5 µm.

Notes: Stolk & Samson (1983: 127) reported ascospores in CBS 328.71; however, we did not observe any ascospores on OA, MEA, CYA or YES after ten weeks incubation at room temperature. Cleistothecia of *P. fuscum*, a closely related species, mature slowly and a longer incubation time also might be needed for *P. tsitsikammaense* (Scott 1968). Another possibility might be that the strain is degenerated after prolonged maintenance.

Penicillium turcosoconidiatum Visagie, Houbraken & K. Jacobs, **sp. nov.** MycoBank MB809977. Fig. 40.

Etymology: Named after the light blue turquoise conidia on MEA.

Diagnosis: *Penicillium turcosoconidiatum* differs from the other species of the *P. fuscum*-clade by its restricted growth on CYA, YES and MEA, short stipes, size of conidia (2–2.5 µm) and turquoise conidial colour (Table 5).

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium fuscum*-clade.

Typus: **South Africa**, Stellenbosch, soil, isolated by C.M. Visagie (holotype CBS H-21876, culture ex-type CBS 138557 = DTO 181-A3 = CV 110 = DAOM 241130).

Barcode and molecular based ID: ITS barcode: KM189645 (alternative markers: *BenA* = KM088889; *CaM* = KM089276; *RPB2* = KM089663).

Description: Colony diam, 7 d, in mm: CYA 15–20; CYA15°C 7–8; CYA30°C 7–10; CYA37°C no growth; MEA 18–25; YES 22–23; DG18 18–19; CYAS 6–8; ratio CYAS:CYA 0.4; CREA no growth, no acid production.

Sporulation on CYA sparse; conidia greyish green, colony texture velutinous, moderately deep, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to brownish orange. Sporulation on YES absent; colony texture floccose, moderately deep, sulcate, orange white colour; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to greyish yellow. Sporulation on DG18 very sparse; conidia greenish white, colony texture floccose, low, plane; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse pale to pale yellow. Sporulation on MEA absent after 7 d; conidia greyish turquoise after prolonged incubation, colony texture velutinous, low, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse yellowish white to brownish orange. Ehrlich reaction negative.

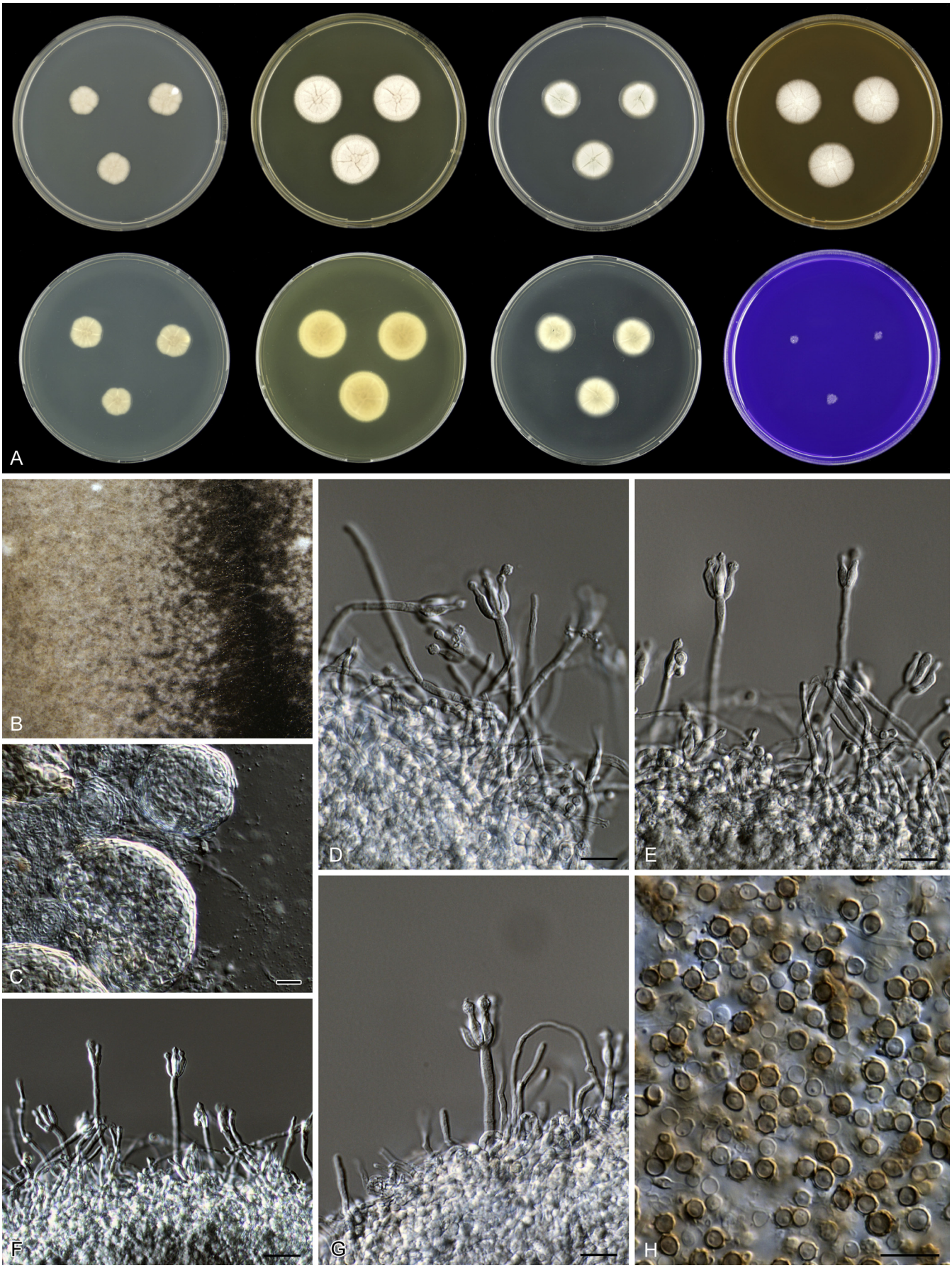

Fig. 39. *Penicillium tsitsikammaense*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–C. Sclerotia. D–G. Conidiophores. H. Conidia. Scale bars = 10 µm.

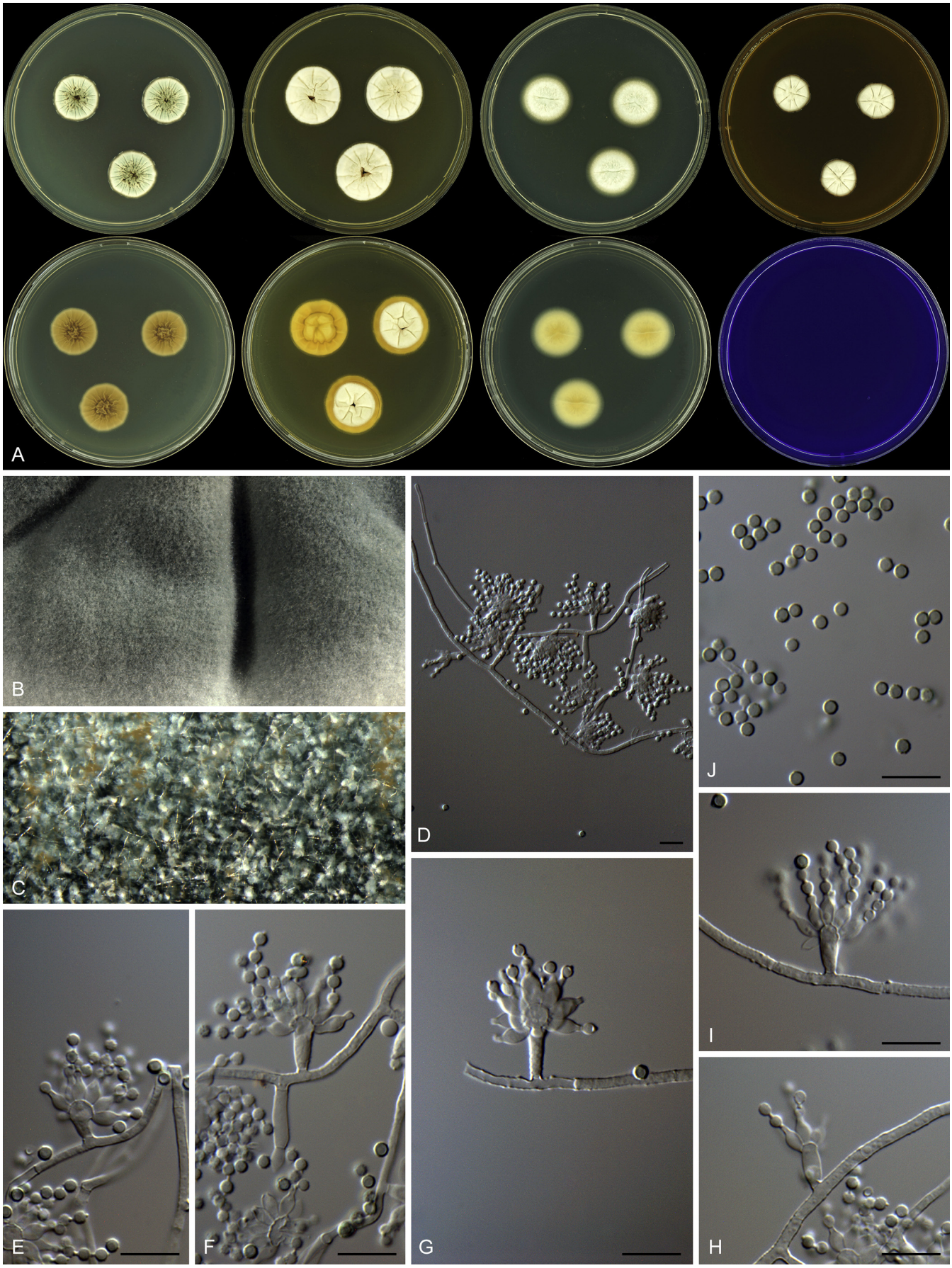

Fig. 40. *Penicillium turcosoconidiatum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B, C. Colony texture. D–I. Conidiophores. J. Conidia. Scale bars = 10 µm.

Sclerotia absent. Conidiophores monoverticillate, mycelia on which conidiophores are borne often rough walled; stipes smooth walled, 6–30 × 1.5–3 µm, vesicles 3–6 µm diam; phialides ampulliform, 12–18 per stipe, 5–6.5 × 2.5–3.5 µm; conidia rough walled, globose, 2–2.5 µm.

Penicillium vagum Houbraken, Pitt, Visagie & K. Jacobs, **sp. nov.** MycoBank MB809978. Fig. 41.

Etymology: Latin, *vagum* = meaning wanderer; named in reference to the phylogenetic relationships of this species, which change according to the different genes analysed.

Diagnosis: This species is phylogenetically distinct. It is characterised by floccose colony texture on CYA, dark green conidia on MEA and distinctly roughened globose conidia.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium vagum*-clade.

Typus: **South Africa**, Western Cape, Stellenbosch mountain, air sample, isolated by C.M. Visagie (holotypus CBS H-21926, cultures ex-type: CBS 137728 = DTO 180-G3 = CV 25 = DAOM 241357).

Barcode and molecular based ID: ITS barcode: KM189642 (alternative markers: *BenA* = KM088886; *CaM* = KM089273; *RPB2* = KM089660).

Description: Colony diam, 7 d, in mm: CYA 30–43; CYA15°C 14–22; CYA30°C 30–31; CYA37°C no growth, sometimes 4 mm; MEA 20–44; YES 34–54; DG18 27–30; CYAS 26–32; ratio CYAS:CYA 0.75–0.85; CREA 20–22, weak to good growth, moderate acid production, no base production.

Sporulation on CYA moderately dense; conidia dull or pure green, colony texture floccose, moderately deep, sulcate; mycelium white; exudate abundant, clear; soluble pigment absent or present, yellow-brown; margin low, narrow, entire; reverse yellowish white to greyish yellow, (yellow-) brown. Sporulation on YES poor to strong; conidia variable, greenish white, dull green or dark green, colony texture floccose, moderately deep, sulcate; mycelium white or yellow; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse light yellow to greyish yellow. Sporulation on DG18 dense; conidia dark green, colony texture velutinous, low, sulcate; mycelium white; exudate absent; soluble pigment not produced; margin low, narrow, entire; reverse transparent, greyish green, pale yellow or pale brown in the centre. Sporulation on MEA dense; conidia dark green (26F5–F8), colony texture velutinous, moderately deep, sulcate; mycelium white; exudate abundant clear; soluble pigment not produced; margin low, narrow, entire; reverse brownish yellow to yellowish brown (5C8–D8). Ehrlich reaction negative.

Sclerotia absent. Conidiophores monoverticillate. Stipes smooth walled, 36–310 × 2.5–3.5 µm, vesicles 4.5–7 µm diam. Phialides ampulliform, 15–20 per stipe, 8.5–11 × 3–4 µm. Conidia conspicuously spiny walled, globose, 2.5–3.5 µm.

Penicillium verhagenii Houbraken, **sp. nov.** MycoBank MB809979. Fig. 42.

Etymology: Named after Cor Verhagen, who assisted with the collection of the soil sample from which the type strain was isolated.

Diagnosis: The species is characterised by the production of long stipes, up to 400 µm, biverticillate conidiophores, restricted growth on CYA at 27 °C and CYAS and bluish green conidia on MEA.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium verhagenii*-clade.

Typus: **Belgium**, Postel, mosses under *Myrica gale* (Bog Myrtle), isolated by J. Houbraken (holotype CBS H-21865, culture ex-type CBS 137959 = DTO 193-A1).

Barcode and molecular based ID: ITS barcode: KM189708 (alternative markers: *BenA* = KM088955; *CaM* = KM089342; *RPB2* = KM089729).

Description: Colony diam, 7 d, in mm: CYA 20–27; CYA15°C 17–25; CYA30°C no growth; CYA37°C no growth; MEA 21–30; YES 28–35; DG18 18–25; CYAS 3–9; ratio CYAS:CYA 0.15–0.30(–0.40); CREA 2–7, weak growth and no acid production.

Sporulation on CYA absent or weakly present in the centre of colony; colony texture velvety to floccose, radially sulcate, deep; conidia pale grey green; mycelium white; exudate absent; soluble pigment absent or poor, pale yellow; margin entire or slightly polygonal in face view; reverse yellow or yellow-brown. Sporulation on YES absent or poor, conidia pale grey green; mycelium white or pale crème; soluble pigment not produced; reverse yellowish brown. Good sporulation on DG18, colony texture velvety; conidia dull green; mycelium inconspicuous in the centre, in some isolates pale yellow at the edge, reverse pale or pale yellow. Good sporulation on MEA, colony texture floccose; conidia blue-green or dull to blue-green; exudate present as pale or yellow droplets; colony reverse not affecting the medium colour, sometimes with yellow centre. Ehrlich reaction negative.

Sclerotia absent. Conidiophores 150–400 µm long, finely rough walled in young parts of the colony, distinctly rough walled in older parts; symmetrically biverticillate, some conidiophores becoming divaricate following having secondary growth of the stipe by sympodial branching at the apex, stipe 3.0–4.5 µm wide. Metulae in terminal whorl of 3–6, of unequal length, 13.0–16.5 × 3.0–4.0 µm. Phialides ampulliform, 2–8 per stipe, 9.0–10 × 3.0–3.5 µm. Conidia in short distorted chains, (broadly) ellipsoidal, roughened, slightly striate, 3.3–4.0 × 2.5–3.3 µm.

Notes: The type strain of *P. rubefaciens* (CBS 145.83^{T}) and two substrains (CBS 146.83 and CBS 147.83) were deposited in the CBS collection by J.A. Quintanilla in 1983. Quintanilla (1982) noted that this species produced floccose sectors and one of the cultures derived from these sectors (CBS 146.83) is identified here as *P. verhagenii*.

Penicillium yezoense Hanzawa ex Houbraken, **sp. nov.** MycoBank MB809980.

= *Penicillium yezoense* Hanzawa, J. Agric. Chem. Soc. Japan: 774. 1943. MB335775 (nom. inval., Art. 39.1.).

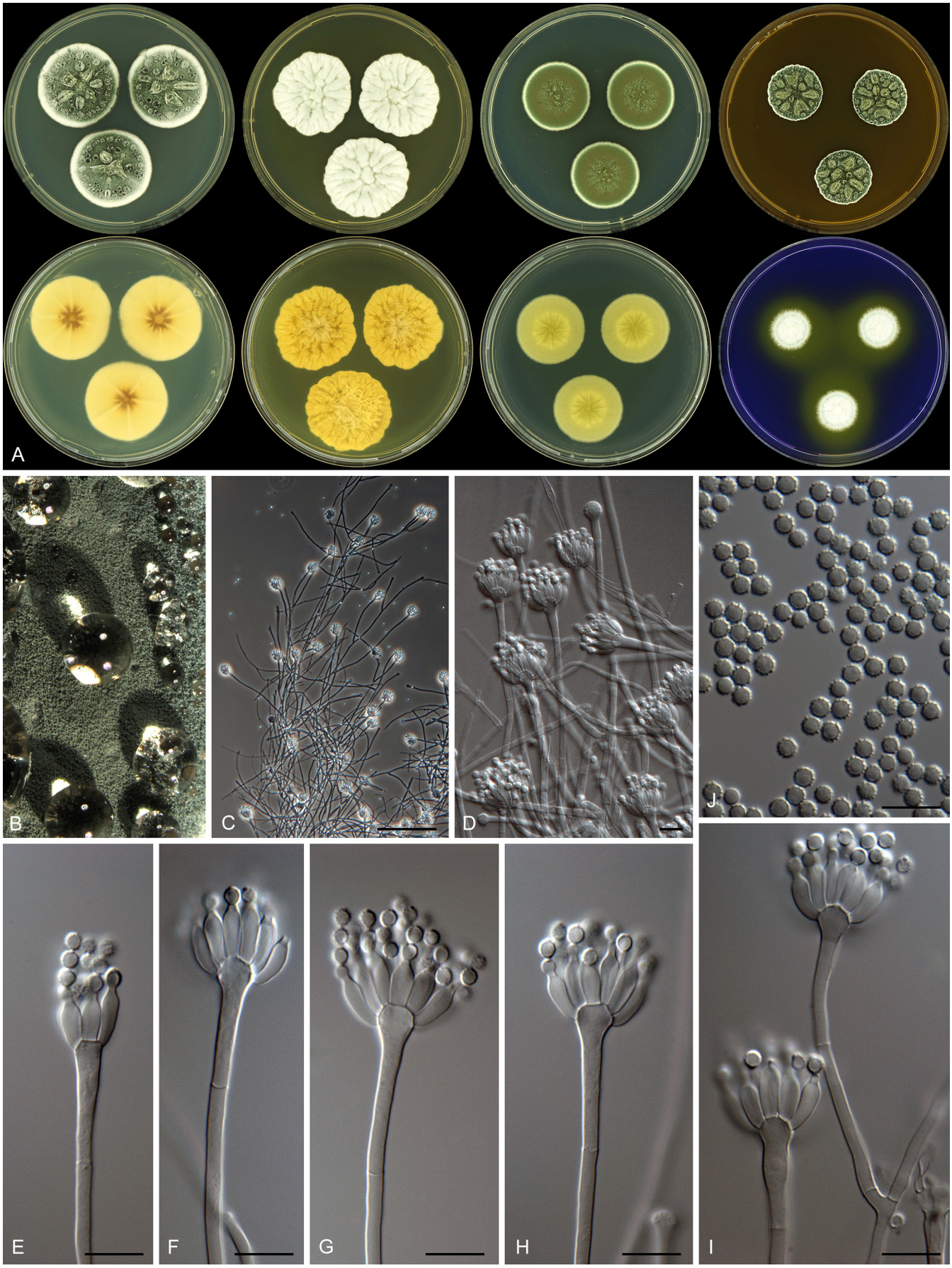

Fig. 41. *Penicillium vagum*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B. Colony texture. C–I. Conidiophores. J. Conidia. Scale bars = 10 µm.

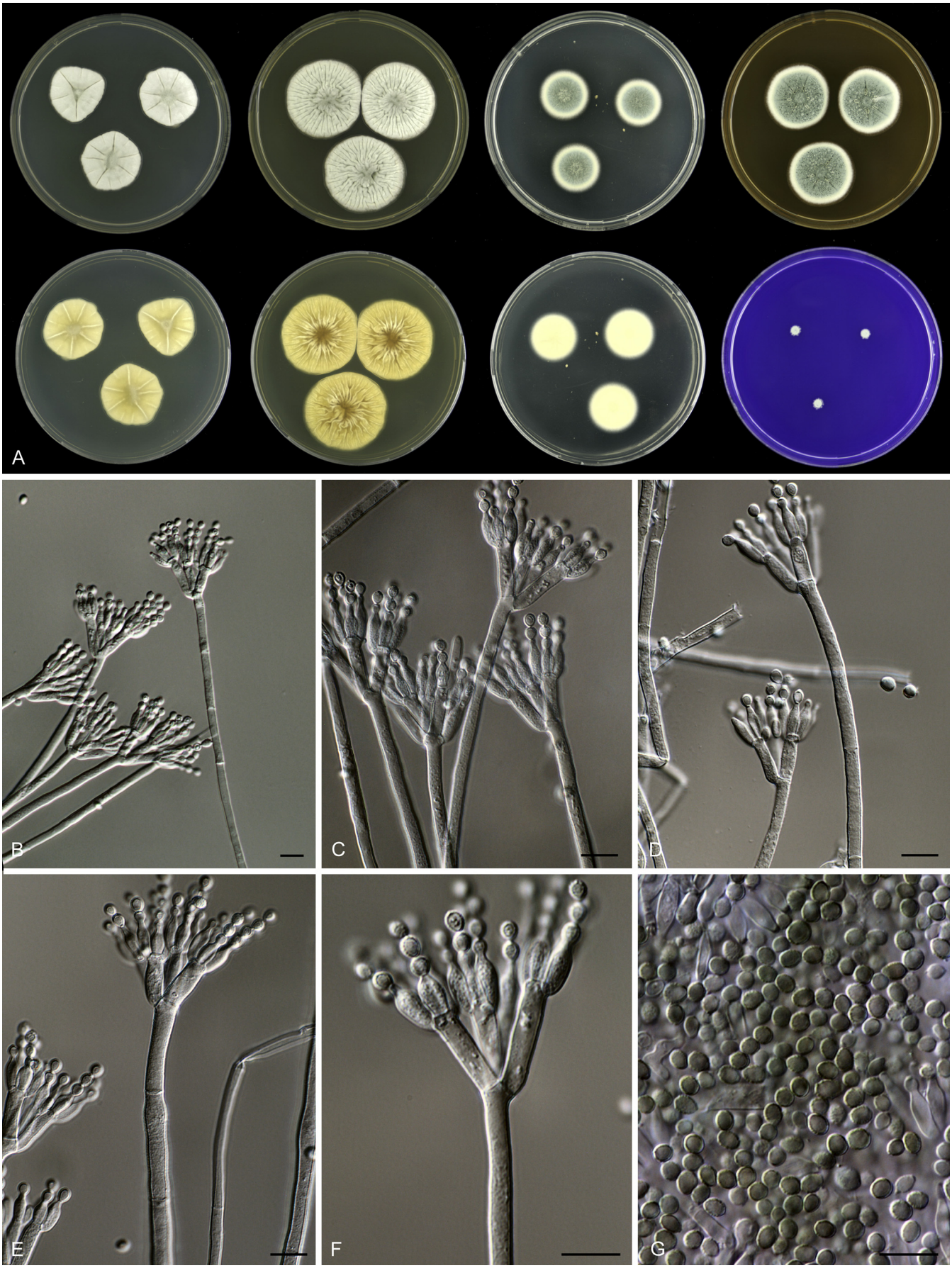

Fig. 42. *Penicillium verhagenii*, A. 7 d old cultures, 25 °C, left to right; first row, all obverse, CYA, YES, DG18, MEA; second row, CYA reverse, YES reverse, DG18 reverse, CREA obverse. B–F. Conidiophores. G. Conidia. Scale bars = 10 µm.

Diagnosis: The species is phenotypically and phylogenetically related to *P. contaminatum*, but differs by a faster growth rate on DG18 (21–25 *vs* 30–39 mm) and CYAS (30–35 *vs* 37–47 mm) and a better sporulation on YES and CYAS. The conidia of *P. yezoense* are ellipsoidal while those of *P. contaminatum* are broadly ellipsoidal.

Typus: **Japan**, butter, isolated by Y. Sasaki (holotype CBS H-21863, culture ex-type CBS 350.59 = ATCC 18333 = FRR 3395 = IFO 5362 = IMI 068615).

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium thomii*-clade.

Barcode and molecular based ID: ITS barcode: KM189553 (alternative markers: *BenA* = KM088792; *CaM* = KM089177; *RPB2* = KM089564).

Notes: *Penicillium yezoense* was described without a Latin diagnosis. To validate the species an English diagnosis is given above, with the name of the original author maintained. This species was considered a synonym of *P. thomii* (Pitt 1980, Ramírez 1982, Pitt *et al.* 2000); however, this study shows that *P. yezoense* is phylogenetically unique (Figs 5, 6).

LIST OF CURRENTLY ACCEPTED SPECIES AND THEIR SYNONYMS IN *PENICILLIUM* SECTION *ASPERGILLOIDES*

The following list includes accepted species in sect. *Aspergilloides* and their synonyms.

Penicillium ardesiacum Novobr., Novosti Sist. Nizsh. Rast. 11: 228. 1974. MB319257.

= *Penicillium thomii* var. *flavescens* S. Abe, J. Gen. Appl. Microbiol. Tokyo 2: 50. 1956. MB347377 (nom. inval., Art. 39.1.).

In: *Penicillium fuscum*-clade

Typus: Kazachstan, Alma-Ata Region, *Vitis vinifera*, T.I. Novobranova. Culture ex-type: IMI 174719 = CBS 497.73 = ATCC 24719 = FRR 1479 = IFO 30540 = IMI 174719 = VKM F-1749.

Penicillium armarii Houbraken, Visagie, Samson & Seifert, this study. MycoBank MB809955.

In: *Penicillium glabrum*-clade

Typus: Australia, Tasmania, Hobart, house dust, collected by G. Gates, 2009, isolated by E. Whitfield and K. Mwange. Culture ex-type: CBS 138171 = DTO 235-F1.

Penicillium athertonense Houbraken, this study. MycoBank MB809956.

In: *Penicillium fuscum*-clade

Typus: Australia, Queensland, Atherton Tableland, forest soil, J. Houbraken & R. van Leeuwen. Culture ex-type: CBS 138161 = DTO 030-C2.

Penicillium aurantioviolaceum Biourge, Cellule 33: 282. 1923. MycoBank MB257885.

In: *Penicillium thomii*-clade

Neotypus: Puerto Rico, unrecorded source, R.A. Toro. Neotype, designated here: CBS H-21954; culture ex-neotype: CBS 137777 = NRRL 762.

Penicillium austroafricanum Houbraken & Visagie, this study. MycoBank MB809957.

In: *Penicillium thomii*-clade

Type: South Africa, Western Cape, Harold Porter Botanical Garden, leaf of *Phaenocoma prolifera*, J. Houbraken & P. Crous. Culture ex-types: CBS 137773 = DTO 133-G5.

Penicillium brunneoconidiatum Visagie, Houbraken & K. Jacobs, this study. MycoBank MB809958.

In: *Penicillium fuscum*-clade

Typus: South Africa, Western Cape, Malmesbury, Riverlands, Fynbos, soil, C.M. Visagie. Culture ex-type: CBS 137732 = DTO 182-E4 = CV 949 = DAOM 241359.

Penicillium bussumense Houbraken, this study. MycoBank MB809959.

In: *Penicillium glabrum*-clade

Typus: the Netherlands, Bussum, Spanderswoud, soil, J. Houbraken. Culture ex-type: CBS 138160 = DTO 018-B2.

Penicillium cartierense Houbraken, this study. MycoBank MB809960.

In: *Penicillium thomii*-clade

Typus: the Netherlands, Eersel, Cartierhiede, soil, J. Houbraken. Culture ex-type: CBS 137956 = DTO 092-H9.

Penicillium clavistipitatum Visagie, Houbraken & K. Jacobs, this study. MycoBank MB809961.

In: *Penicillium fuscum*-clade

Typus: South Africa, Malmesbury, Riverlands, Fynbos, soil, C.M. Visagie. Culture ex-type: CBS 138650 = DTO 182-E5 = CV 336 = KAS 4112 = DAOM 241092.

Penicillium contaminatum Houbraken, this study. MycoBank MB809962.

In: *Penicillium thomii*-clade

Typus: United Kingdom, Kew, Surrey, culture contaminant. Culture ex-type CBS 345.52 = DTO 091-A3 = IMI 049057.

Penicillium crocicola W. Yamam., Sci. Rep. Hyogo Univ. Agric. 2: 28. 1956. MycoBank MB302391.

In: *Penicillium thomii*-clade

Type: Japan, corm of *Crocus sativus*, W. Yamamoto. Culture ex-type: CBS H-7528 = CBS 745.70 = ATCC 18313 = QM 7778.

Penicillium flavisclerotiatum Visagie, Houbraken & K. Jacobs, this study. MycoBank MB809963.

In: *Penicillium fuscum*-clade

Typus: South Africa, Western Cape, Stellenbosch mountain, Fynbos, soil, isolated by C.M. Visagie. Culture ex-type: CBS 137750 = DTO 180-I8 = CV 100 = DAOM 241157.

Penicillium frequentans Westling, Ark. Bot. 11: 133. 1911. MycoBank MB152118.

= *Penicillium paczoskii* K.M. Zaleski, Bull. Int. Acad. Polon. Sci., Sér. B 1927: 505. 1927. MB273253.

In: *Penicillium glabrum*-clade

Typus: Unknown source, K. Westling. CBS 105.11.

Penicillium fuscum (Sopp) Biourge, Cellule 33: 103. 1923. MycoBank MB289082.

≡ *Citromyces fuscus* Sopp, Skr. Vidensk.-Selsk. Christiana Math.-Nat. Kl. 11: 120. 1912. MB178643.
= *Penicillium silvaticum* Suprun, Byull. Mosk. Obshch. Ispyrt. Prir.: 90. 1956. MB492648.
= *Penicillium pinetorum* M. Chr. & Backus, Mycologia 53: 457. 1961. MB335758.
= *Penicillium macedoniense* Verona & Mick., Mycopathol. Mycol. Appl. 18: 289. 1962. MB335746.
= *Eupenicillium pinetorum* Stolk, Antonie van Leeuwenhoek 34: 37. 1968. MB330740.
= *Penicillium lapatayae* C. Ramírez, Mycopathologia 91: 96. 1985. MB105610.
= *Eladia inflata* Y.L. Jiang & T.Y. Zhang, Mycotaxon 108: 128. 2009. MB512859.

In: *Penicillium fuscum*-clade

Neotypus: USA, Wisconsin, pine-birch forest soil, Vilas County, M. Christensen. Culture ex-neotype: WSF 15-C = CBS 295.62 = ATCC 14770 = CCRC 31517 = DSM 2438 = IFO 7743 = IMI 094209 = MUCL 31196 = NRRL 3008.

Notes: The type culture of *P. lapatayae* maintained in the CBS collection (CBS 203.87) is dead. The IBT culture collection contains two ex-type isolates, one directly sent by C. Ramírez to the IBT collection (IJFM 19012 = IBT 10870 = DTO 297-C8) and another received the ATCC (ATCC 60197 = IBT 16267 = DTO 297-C9). IBT 16267 is identified here as *P. fuscum* (Figs 12, 13) and IBT 10870 as *P. adametzioides*. Neither strain formed the pink soft sclerotia described in the original description. However, IBT 16267 resembles the original description best because this isolate produces conspicuously ornamented subglobose conidia and pure to dark green conidia on MEA. In contrast, IBT 10870 produces broadly ellipsoidal, smooth to finely roughened conidia, and grey-green colonies on MEA. Based on this data, we consider *P. lapatayae* a synonym of *P. fuscum*.

Penicillium fusisporum L. Wang, PLoS ONE 9:e101454-P2. 2014. MB806119.

In: *Penicillium thomii*-clade

Typus: China, Shaanxi, Nangongshan Forest Park, leaves of *Rhododendron* sp., P-J Han. Culture ex-type: HMAS 244961 = CBS 137463 = AS3.15338 = NRRL 62805.

Penicillium glabrum (Wehmer) Westling, Ark. Bot. 11: 131. 1911. MB120545.

≡ *Citromyces glaber* Wehmer, Beitr. Kenntn. Einh. Pilze 1: 24. 1893. MB178959.
= *Citromyces pfefferianus* Wehmer, Ber. Deutsch. Bot. Ges. 11: 333. 1893. MB157685.
= *Penicillium aurantiobrunneum* Dierckx, Ann. Soc. Sci. Bruxelles 25: 86. 1901. MB237393.
?= *Penicillium fluitans* Tiegs, Ber. Deutsch. Bot. Ges. 37: 500. 1919. MB151731; *fide* Raper & Thom (1949) and Pitt (1980). No culture examined.
= *Penicillium flavidorsum* Biourge, Cellule 33: 290. 1923. MB265032.
= *Penicillium oledzkii* K.M. Zaleski, Bull. Int. Acad. Polon. Sci., Sér. B., Sci. Nat. 1927: 499. 1927. MB272809.
= *Penicillium terlikowskii* K.M. Zaleski, Bull. Int. Acad. Polon. Sci., Sér. B., Sci. Nat. 1927: 501. 1927. MB280026.
= *Penicillium spinuloramigenum* Y. Sasaki, J. Appl. Mycol., Japan: 58. 1946. MB302426 (nom. inval., Art. 39.1.).
= *Penicillium spinuloramigenum* Y. Sasaki ex C. Ramírez, Manual and Atlas of the Penicillia: 162. 1982. MB115801.

In: *Penicillium glabrum*-clade

Neotypus: unrecorded source, K. Westling. Culture ex-neotype: IMI 91944 = IMI 91944 = CBS 125543.

Penicillium grancanariae C. Ramírez, A.T. Martínez & Ferrer, Mycopathologia 66: 79. 1978. MycoBank MB319273.

In: *Penicillium spinulosum*-clade

Typus: Spain, Canary Islands, Gran Canaria, air. Culture ex-type: IJFM 3745 = CBS 687.77 = IJFM 3745 = IMI 253783.

Penicillium grevilleicola Houbraken & Quaedvlieg, this study. MycoBank MB809964.

In: *Penicillium thomii*-clade

Typus: Australia, Kangaroo Island, Kingscote, leaf of *Grevillea ilicifolia*, J. Houbraken & W. Quaedvlieg. Culture ex-type: CBS 137775 = DTO 174-E6.

Penicillium hoeksii Houbraken, this study. MycoBank MB809965.

In: *Penicillium hoeksii*-clade

Typus: Belgium, Postel, soil under Compact Rush (*Juncus conglomeratus*), J. Houbraken. Culture ex-type: CBS 137776 = DTO 192-H4.

Penicillium infra-aurantiacum Visagie, Houbraken & K. Jacobs, this study. MycoBank MB809966.

In: *Penicillium sublectaticum*-clade

Typus: South Africa, Western Cape, Malmesbury, Riverlands, bracts of *Protea repens* infructescence, C.M. Visagie. Culture ex-type: CBS 137747 = DTO 183-C3 = CV 1518 = DAOM 241145.

Penicillium jejuense M.S. Park & Y.W. Lim, submitted. MycoBank MB808392.

In: *Penicillium thomii*-clade

Typus: Republic of Korea, Jeju Island, *Pollicipes mitella*. Culture ex-type: SFC20140101-M756T.

Penicillium kananaskense Seifert, Frisvad & McLean, Can. J. Bot. 72: 20. 1994. MB362160.

In: *Penicillium lividum*-clade

Typus: Canada, Alberta, Kananaskis Valley, soil, FH horizon, in a *Pinus contorta* var. *latifolia* forest, M.A. McLean. Culture ex-type: CBS 530.93 = ATCC 90282 = DAOM 216105 = IBT 11775 = IMI 356791.

Penicillium kiamaense Houbraken & Pitt, this study. MycoBank MB809967.

In: undefined clade (basal to *P. glabrum* and *P. thomii*-clade).

Typus: Australia, NSW, Barren Grounds Nature Reserve, near Kiama, soil, J.I. Pitt. Culture ex-type: CBS 137947 = FRR 6087 = DTO 056-I6.

Penicillium lividum Westling, Ark. Bot. 11: 134. 1911. MycoBank MB178817.

In: Penicillium lividum-clade

Neotypus: Unrecorded source, Scotland. Culture ex-neotype: IMI 39736 = CBS 347.48 = ATCC 10102 = CCRC 31286 = DSM 1180 = IFO 6102 = NRRL 754 = QM 1930 = VKM F-303.

Note: Some sub-cultures of the ex-neotype culture of *P. lividum* received from a few collections were contaminated with *P. spinulosum*. Through the courtesy of Dr. John David, former curator of IMI, we re-examined the neotype specimen IMI 39736 and confirmed that it conforms to the concept of this species proposed by Pitt (1980), and the more restricted concept adopted in this paper.

Penicillium longicatenatum Visagie, Busby, Houbraken & K. Jacobs, this study. MycoBank MB809968.

In: *Penicillium vagum*-clade

Typus: South Africa, Western Cape, Malmesbury, Riverlands, Fynbos, soil, C.M. Visagie. Culture ex-type: CBS 137735 = DTO 180-D9 = CV 2847 = DAOM 241119.

Penicillium malmesburiense Visagie, Houbraken & K. Jacobs, this study. MycoBank MB809969.

In: *Penicillium sublectaticum*-clade

Typus: South Africa, Western Cape, Malmesbury, Riverlands, mite from *Protea repens* infructescence, C.M. Visagie. Culture ex-type: CBS 137744 = DTO 182-H5 = CV 1180 = DAOM 241144.

Penicillium montanense M. Chr. & Backus, Mycologia 54: 574. 1962. MycoBank MB335752.

= *Penicillium echinosporum* G. Sm., Trans. Brit. Mycol. Soc. 45: 387. 1962. MB335724 (nom. illeg., Art. 53).

= *Penicillium asperosporum* G. Sm., Trans. Brit. Mycol. Soc. 48: 275. 1965. MB335714.

In: *Penicillium fuscum*-clade

Typus: USA, Montana, Ravalli County Lodgepole, pine-Douglas fir soil. Culture ex-type: CBS 310.63 = ATCC 14941 = FRR 3407 = IFO 7740 = IHEM 4375 = IMI 099468 = MUCL 31326 = NRRL 3407.

Notes: There is some taxonomic confusion around *P. echinosporum* and *P. asperosporum*. *Penicillium echinosporum* Nehira was described in 1933 without a Latin diagnosis. The name was incorrectly validated by Ramírez (1982) but Latin descriptions were compulsory only after 1935. Samson *et al.* (2011) showed that the type of this species (CBS 344.51^{T}) belongs to *Talaromyces* and the combination *Talaromyces echinosporus* was proposed. Currently, this species is placed in synonymy with *Talaromyces rugulosus* (Yilmaz *et al.* 2014). In 1962, unaware of the existence *P. echinosporum* Nehira, Smith described *P. echinosporum* G. Sm. and typified it with IMI 080450^{T}. Three years later he corrected this error and renamed his species *P. asperosporum*. Sequence analysis confirm that NRRL 3411 (= IMI 080450^{T}) is conspecific with *P. montanense*.

Penicillium odoratum M. Chr. & Backus, Mycologia 53: 459. 1961. MycoBank MB335755.

= *Penicillium trzebinskianum* S. Abe, J. Gen. Appl. Microbiol., Tokyo 2: 63. 1956. MB302427.

= *Penicillium trzebinskianum* S. Abe ex C. Ramírez, Manual and Atlas of the Penicillia: 79. 1982. MB115803.

In: *Penicillium lividum*-clade

Typus: USA, Wisconsin, soil, spruce-larch bog, M. Christensen. Culture ex-type: WSF 2000 = DTO 205-B7 = CBS 294.62 = CBS 129423 = DAOM 226269 = ATCC 14769 = DSM 2419 = IFO 7741 = IMI 094208ii = NRRL 3007 = DAOM 226269.

Penicillium palmense C. Ramírez & A.T. Martínez, Mycopathologia 66: 80. 1978. MycoBank MB319289.

In: *Penicillium spinulosum*-clade

Typus: Air, Canary Islands, Gran Canaria, Spain. Culture ex-type: IJFM 3840 = CBS 336.79 = ATCC 38669 = VKM F-2181.

Penicillium pulvis Houbraken, Visagie, Samson & Seifert, this study. MycoBank MB809970.

In: *Penicillium glabrum*-clade

Typus: **South Africa**, South Africa, Kuils River, house dust, K. Jacobs. Culture ex-type: CBS 138432 = DTO 180-B7.

Penicillium purpurescens (Sopp) Raper & Thom, A manual of the Penicillia: 177. 1949. MycoBank MB335761.

≡ *Citromyces purpurescens* Sopp, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 11: 117. 1912. MB157120.
?= *Citromyces viridо-albus* Sopp, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 11: 131. 1912. MB454083; *fide* Raper & Thom (1949); no culture available.
?= *Penicillium viridо-album* (Sopp) Biourge, Cellule 33: 106. 1923. MB492659; *fide* Raper & Thom (1949).
= *Penicillium internascens* Szilvinyi, Zentralbl. Bakteriol. Parasitenk., Abt. 2 103: 148. 1941. MB289091.
= *Penicillium resinae* Z.T. Qi & H.Z. Kong, Acta Mycol. Sin.: 103. 1982. MB110236.

In: *Penicillium glabrum*-clade

Neotypus: Canada, soil, G.R. Bisby. Culture ex-neotype: IMI 39745 = CBS 366.48 = ATCC 10485 = NRRL 720 = QM 1959.

Penicillium quercetorum Baghd., Novosti Sist. Nizsh. Rast. 5: 110. 1968. MB335762.

In: *Penicillium quercetorum*-clade

Typus: Syria, soil near Es-Euveida, V.C. Baghdadi. Culture ex-type: CBS H-7527 = CBS 417.69 = ATCC 48727 = CCRC 31668 = FRR 516 = IFO 31749 = IMI 140342 = MUCL 31203 = VKM F-1074.

Penicillium ranomafanaense Houbraken & Hagen, this study. MycoBank MB809971.

In: *Penicillium verhagenii*-clade

Typus: Madagascar, Ranoma fana, soil, F. Hagen & J. Houbraken. Culture ex-type: CBS 137953 = DTO 085-A5.

Penicillium roseomaculatum Biourge, Cellule 33: 301. 1923. MycoBank MB276785.

= *Penicillium baiicola* Biourge, Cellule 33: 305. 1923. MB258101.
= *Penicillium subericola* Barreto, Frisvad & Samson, Fungal Diver. 49: 32. 2011. MB517383

In: *Penicillium spinulosum*-clade

Typus: Unrecorded source, P. Biourge. Culture ex-type: CBS 137962 = NRRL 728 = FRR 0728 = IMI 189696 = MUCL 29101.

Penicillium roseoviride Stapp & Bortels, Zentralbl. Bakteriol. Parasitenk., Abt. 2 93: 51. 1935. MycoBank MB492646.

In: *Penicillium thomii*-clade

Typus: Germany, soil in a beech forest. Culture ex-type: CBS 267.35 = ATCC 10412 = IFO 6089 = IMI 039740ii = NRRL 760 = QM 7485).

Penicillium rudallense Houbraken, Visagie & Pitt, this study. MycoBank MB809972.

In: *Penicillium glabrum*-clade

Typus: Australia, WA, Rudall River National Park, soil, A.D. Hocking. Culture ex-type: CBS 138162 = FRR 6085 = DTO 056-I4.

Penicillium saturniforme (L. Wang & W.Y. Zhuang) Houbraken & Samson, Stud. Mycol. 70: 48. 2011. MycoBank MB561958.

≡ *Eupenicillium saturniforme* L. Wang & W.Y. Zhuang, Mycopathologia 167: 300. 2009. MB541663.

In: *Penicillium saturniforme*-clade

Typus: China, Jiling Province, Dunhua Little Peony Forest Reserve, soil. Culture ex-type: AS 3.6886 = CBS 122276 = HMAS 130355-1-4.

Penicillium spinulosum Thom, U.S.D.A. Bur. Animal Industr. Bull. 118: 76. 1910. MycoBank MB215401.

= *Penicillium pfefferianum* (Wehmer) Westling, Ark. Bot. 11: 132. 1911. MB492636.
= *Penicillium flavocinereum* Biourge, Cellule 33: 293. 1923. MB265060.
?= *Penicillium janthocitrinum* Biourge, Cellule 33: 311. 1923. MB119135; *fide* Pitt (1980).
= *Penicillium mucosum* Stapp & Bortels, Zentralbl. Bakteriol. Parasitenk., Abt. 2 93: 51. 1935. MB492626.
= *Penicillium tannophilum* Stapp & Bortels, Zentralbl. Bakteriol. Parasitenk., Abt. 2 93: 52. 1935. MB492654.
= *Penicillium brunneoviride* Szilvinyi, Zentralbl. Bakteriol. Parasitenk., Abt. 2 103: 144. 1941. MB289078.
= *Penicillium trzebinskii* var. *magnum* Sakag. & S. Abe, J. Gen. Appl. Microbiol., Tokyo 2: 62. 1956. MB352367.
= *Penicillium abeanum* G. Sm., Trans. Brit. Mycol. Soc. 46: 333. 1963. MB335704.

In: *Penicillium spinulosum*-clade

Neotypus: Germany, Hannover, culture contaminant, C. Wehmer. Culture ex-neotype: IMI 24316i = CBS 374.48 = ATCC 10498 = FRR 1750 = MUCL 13910 = MUCL 13911 = NCTC 591 = NRRL 1750 = QM 7654.

Penicillium sterculiniicola Houbraken, this study. MycoBank MB809973.

In: *Penicillium spinulosum*-clade

Typus: USA, spawn run compost. Culture ex-type: CBS 122426 = DTO 031-A4.

Penicillium sublectaticum Houbraken, Frisvad, Samson & Seifert, this study. MycoBank MB809974.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *P. sublectaticum*-clade.

Typus: New Zealand, Dunedin, house dust, collected by T. Atkinson, 2009, isolated by E. Whitfield and K. Mwange. Culture ex-type: CBS 138217 = DTO 244-G2.

Penicillium subspinulosum Houbraken, this study. MycoBank MB809975.

In: subgenus *Aspergilloides*, section *Aspergilloides*, *Penicillium spinulosum*-clade.

Typus: Poland, soil, J. Houbraken & B. Byskal. Culture ex-type CBS 137946 = DTO 041-F2.

Penicillium thiersii S.W. Peterson, E.M. Bayer & Wicklow, Mycologia 96: 1283. 2005. MycoBank MB487738.

In: *Penicillium thiersii*-clade

Typus: USA, Wisconsin, New Glarus Woods State Park, old black stroma of *Hypoxylon* encrusting the surface of a dead maple log, H.D. Thiers. Culture ex-type: BPI 842269 = CBS 117503 = IBT 27050 = NRRL 28162.

Penicillium thomii Maire, Bull. Soc. Hist. Nat. Afrique N. 8: 189. 1917. MycoBank MB202819.

?= *Penicillium parallelosporum* Y. Sasaki, J. Fac. Agric. Hokkaido Imp. Univ. 49: 147. 1950. MB302414 (nom. inval., Art. 39.1.).
= *Penicillium patens* Pitt & A.D. Hocking, Mycotaxon 22: 197. 1985. MB105611.

In: *Penicillium thomii*-clade

Neotypus: USA, Spaulding, pine cone. Culture ex-neotype: IMI 189694 = CBS 225.81 = NRRL 2077.

Penicillium trzebinskii K.M. Zaleski, Bull. Int. Acad. Polon. Sci., Sér. B., Sci. Nat. 1927: 498. 1927. MycoBank MB280795.

= *Penicillium tannophagum* Stapp & Bortels, Zentralbl. Bakteriol. Parasitenk., Abt. 2 93: 52. 1935. MB492653.
= *Penicillium mediocre* Stapp & Bortels, Zentralbl. Bakteriol. Parasitenk., Abt. 2 93: 50. 1935. MB492624.
= *Penicillium toxicarium* I. Miyake ex C. Ramírez, Manual and Atlas of the Penicillia: 125. 1982. MB115802.

In: *Penicillium spinulosum*-clade

Typus: Poland, Poznan area, Dluga Goslina Forest, soil, K. Zaleski. Culture ex-type: CBS 382.48 = ATCC 10507 = FRR 731 = IFO 6110 = IMI 039749 = MUCL 29102 = NRRL 731 = QM 7678.

Penicillium tsitsikammaense Houbraken, this study. MycoBank MB809976.

In: *Penicillium fuscum*-clade

Typus: South Africa, Cape Province, Tsitsikamma Forest near Knysna, forest soil, D.B. Scott. Culture ex-type: CBS 328.71 = DTO 006-I3 = CSIR 1092.

Penicillium turcosoconidiatum Visagie, Houbraken & K. Jacobs, this study. MycoBank MB809977.

In: *Penicillium fuscum*-clade

Typus: South Africa, Stellenbosch, soil, C.M. Visagie. Culture ex-type: CBS 138557 = DTO 181-A3 = CV 110 = DAOM 241130.

Penicillium vagum Houbraken, Pitt, Visagie & K. Jacobs, this study. MycoBank MB809978.

In: *Penicillium vagum*-clade

Typus: South Africa, Western Cape, Stellenbosch mountain, air sample, C.M. Visagie. Culture ex-type: CBS 137728 = DTO 180-G3 = CV 25 = DAOM 241357.

Penicillium valentinum C. Ramírez & A.T. Martínez, Mycopathologia 72: 183. 1980. MycoBank MB113027.

In: *Penicillium thomii*-clade

Typus: Spain, Madrid, air. C. Ramírez. Culture ex-type: IJFM 5071 = CBS 172.81.

Penicillium verhagenii Houbraken, this study. MycoBank MB809979.

In: *Penicillium verhagenii*-clade

Typus: Belgium, Postel, mosses under *Myrica gale* (Bog Myrtle), J. Houbraken. Culture ex-type CBS 137959 = DTO 193-A1.

Penicillium yezoense Hanzawa ex Houbraken, this study. MycoBank MB809980.

= *Penicillium yezoense* Hanzawa, J. Agric. Chem. Soc. Japan: 774. 1943. MB335775 (nom. inval., Art. 39.1.).

In: *Penicillium thomii*-clade

Typus: Japan, butter, Y. Sasak. Culture ex-type: CBS 350.59 = ATCC 18333 = FRR 3395 = IFO 5362 = IMI 068615.

Penicillium zhuangii L. Wang, PLoS ONE 9 e101454-P4. 2014. MycoBank MB805945.

In: *Penicillium hoeksii*-clade

Typus: China, Shaanxi, Nangongshan Forest Park, leaves of *Rhododendron* sp., 1 500 m, P-J Han. Culture ex-type: HMAS 244961 = CBS 137464 = AS3.15338 = NRRL 62806.

ACKNOWLEDGEMENTS

This research was in part supported by grants from the Alfred P. Sloan Foundation Program on the Microbiology of the Built Environment. The research of Karin Jacobs was funded by a grant from the South African Biosystematics Initiative (SABI) of the National Research Foundation (NRF), South Africa. We are grateful to the many collectors of soil samples and house dust samples that yielded many of the new species described here. Uwe Braun is acknowledged for his advice on the new species names and the nomenclatural issues. We are grateful to John David, former curator of herb. IMI, for sending us a microscopic preparation from the neotype specimen of *P. lividum*.

REFERENCES

Barreto MC, Houbraken J, Samson RA, *et al*. (2011). Taxonomic studies of the *Penicillium glabrum* complex and the description of a new species *P. subericola*. *Fungal Diversity* **49**: 23–33.

Biourge P (1923). Les moisissures du groupe *Penicillium* Link. *Cellule* **33**: 7–331.

Frisvad JC, Houbraken J, Popma S, *et al*. (2013). Two new *Penicillium* species *P. buchwaldii* and *P. spathulatum*, producing the anticancer compound asperphenamate. *FEMS Microbiology Letters* **339**: 77–92.

Frisvad JC, Samson RA, Stolk AC (1990). Disposition of recently described species in *Penicillium*. *Persoonia* **14**: 209–232.

Hetherington AC, Raistrick H (1931). Studies in the biochemistry of microorganisms XI. On citromycetin, a new yellow colouring matter produced from glucose by a species of *Citromyces*. *Philosophical Transactions of the Royal Society, London, Series B* **220**: 209–244.

Houbraken J, Frisvad JC, Samson RA (2011a). Fleming's penicillin producing strain is not *Penicillium chrysogenum* but *P. rubens*. *IMA Fungus* **2**: 87–95.

Houbraken J, Frisvad JC, Samson RA (2011b). Taxonomy of *Penicillium* section *Citrina*. *Studies in Mycology* **70**: 53–138.

Houbraken J, Frisvad JC, Seifert KA, *et al*. (2012a). New penicillin-producing *Penicillium* species and an overview of section *Chrysogena*. *Persoonia* **29**: 78–100.

Houbraken J, Samson RA (2011). Phylogeny of *Penicillium* and the segregation of *Trichocomaceae* into three families. *Studies in Mycology* **70**: 1–51.

Houbraken J, Spierenburg H, Frisvad JC (2012b). *Rasamsonia*, a new genus comprising thermotolerant and thermophilic *Talaromyces* and *Geosmithia* species. *Antonie van Leeuwenhoek* **101**: 403–421.

Li C, Gloer JB, Wicklow DT (2003). Thiersindoiloes A-C: new indole diterpenoids from *Penicillium thiersii*. *Journal of Natural Products* **66**: 1232–1235.

Li C, Gloer JB, Wicklow DT, *et al*. (2002). Thiersinines A and B: novel anti-insectan indole diterpenoids from a new fungicolous *Penicillium* species (NRRL 28147). *Organic Letters* **4**: 3095–3098.

Li C, Gloer JB, Wicklow DT, *et al*. (2005). Antiinsectan decaturin and oxalicine analogues from *Penicillium thiersii*. *Journal of Natural Products* **68**: 319–322.

Librado P, Rozas J (2009). DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25**: 1451–1452.

Lund F (1995). Differentiating *Penicillium* species by detection of indole metabolites using a filter paper method. *Letters in Applied Microbiology* **20**: 228–231.

Mahmoodian A, Stickings CE (1964). 15 metabolites of *Penicillium frequentans* Westling, isolation of sulochrin, asterric acid, (+)-bisdecchlorogeodin + 2 new substituted anthraquinones questin + questinol. *Biochemical Journal* **92**: 369–378.

Nylander JAA (2004). *MrModeltest v2. Program distributed by the author.* Evolutionary Biology Centre, Uppsala University.

Park MS, Fong JJ, Oh SY, *et al. Penicillium jejuense* sp. nov., isolated from the marine environments of Jeju Island, Korea. Submitted.

Peterson SW (2000). Phylogenetic analysis of *Penicillium* species based on ITS and LSU-rDNA nucleotide sequences. In: *Integration of modern taxonomic methods for Penicillium and Aspergillus classification* (Samson RA, Pitt JI, eds). Harwood Academic Publishers, Amsterdam: 163–178.

Peterson SW, Bayer EM, Wicklow DT (2004). *Penicillium thiersii*, *Penicillium angulare* and *Penicillium decaturense*, new species isolated from wood-decay fungi in North America and their phylogenetic placement from multilocus DNA sequence analysis. *Mycologia* **96**: 1280–1293.

Pitt JI (1980 ["1979"]). *The genus Penicillium and its teleomorphic states Eupenicillium and Talaromyces*. Academic Press Inc, London.

Pitt JI, Hocking AD (1985). New species of fungi from Indonesian dried fish. *Mycotaxon* **22**: 197–208.

Pitt JI, Klich MA, Shaffer GP, *et al*. (1990). Differentiation of *Penicillium glabrum* from *Penicillium spinulosum* and other closely related species: an integrated taxonomic approach. *Systematic and Applied Microbiology* **13**: 304–309.

Pitt JI, Samson RA, Frisvad JC (2000). List of accepted species and their synonyms in the family *Trichocomaceae*. In: *Integration of modern taxonomic methods for Penicillium and Aspergillus classification* (Samson RA, Pitt JI, eds). Harwood Academic Publishers, Amsterdam: 9–79.

Quintanilla JA (1982). Three new species of *Penicillium* isolated from soil. *Mycopathologia* **80**: 73–82.

Ramírez C (1982). *Manual and atlas of the Penicillia*. Elsevier Biomedical Press, Amsterdam.

Raper K, Thom C (1949). *A manual of the penicillia*. The Williams & Wilkins Company, Baltimore.

Ronquist F, Huelsenbeck JP (2003). MrBayes version 3.0: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Samson RA, Houbraken J, Thrane U, *et al*. (2010). *Food and indoor fungi*. In: *CBS Laboratory manual*.

Samson RA, Seifert KA, Kuijpers A, *et al*. (2004). Phylogenetic analysis of *Penicillium* subgenus *Penicillium* using partial B-tubulin sequences. *Studies in Mycology* **49**: 175–200.

Samson RA, Yilmaz N, Houbraken J, *et al*. (2011). Phylogeny and nomenclature of the genus *Talaromyces* and taxa accommodated in *Penicillium* subgenus *Biverticillium*. *Studies in Mycology* **70**: 159–183.

Schoch CL, Seifert KA, Huhndorf S, *et al*. (2012). Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 6241–6246.

Scott DB (1968). The genus *Eupenicillium* Ludwig. *CSIR Research Report* **272**: 1–150.

Seifert KA, Frisvad JC, McLean MA (1994). *Penicillium kananaskense*, a new species from Alberta soil. *Canadian Journal of Botany* **72**: 20–24.

Skouboe P, Frisvad JC, Taylor JW, *et al*. (1999). Phylogenetic analysis of nucleotide sequences from the ITS region of terverticillate *Penicillium* species. *Mycological Research* **103**: 873–881.

Stamatakis A, Hoover P, Rougemont J (2008). A rapid bootstrap algorithm for the RAxML Web-Servers. *Systematic Biology* **75**: 758–771.

Stolk AC (1968). Studies on the genus *Eupenicillium* Ludwig. III. Four new species of *Eupenicillium*. *Antonie van Leeuwenhoek* **34**: 37–53.

Stolk AC, Samson RA (1983). The Ascomycete genus *Eupenicillium* and related *Penicillium* anamorphs. *Studies in Mycology* **23**: 1–149.

Subramanian CV (1971). *Hyphomycetes: an account of Indian species except Cercosporae*. Indian Council of Agricultural Research, New Delhi.

Taylor JW, Jacobson DJ, Kroken S, *et al*. (2000). Phylogenetic species recognition and species concepts in fungi. *Fungal Genetics and Biology* **31**: 21–32.

Visagie CM, Houbraken J, Frisvad JC, *et al*. (2014). Identification and nomenclature of the genus *Penicillium*. *Studies in Mycology* **78**: 343–371.

Wang B, Yu Y, Wang L (2014). *Penicillium fusisporum* and *P. zhuangii*, two new monoverticillate species with apical-swelling stipes of section *Aspergilloides* isolated from plant leaves in China. *PLoS ONE* **9**: e101454.

Wang L, Zhuang W-Y (2009). *Eupenicillium saturniforme*, a new species discovered from northeast China. *Mycopathologia* **167**: 297–305.

Yilmaz N, Visagie CM, Houbraken J, *et al*. (2014). Polyphasic taxonomy of the genus *Talaromyces*. *Studies in Mycology* **78**: 175–341.

Zaleski KM (1927). Über die in Polen gefundenen Arten der Gruppe Penicillium Link. I, II and III Teil. *Bulletin de l'Académie Polonaise des Sciences et des Lettres, Classe des Sciences Mathématiques et Naturelles – Série B: Sciences Naturelles*: 417–563, pls 36–44 (printed in 1928).